

**SEMINAR REPORT**

**Viral Symbionts of Parasitoids**

By

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(2018-11- 033)

Presented on 13/12/2019

**Submitted in partial fulfilment for requirement of course**

**ENT 591: Masters Seminar (0+1)**



**DEPARTMENT OF AGRICULTURAL ENTOMOLOGY**

**COLLEGE OF HORTICULTURE**

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## DECLARATION

I, Abinsha Ashraf (2018-11-033) hereby declare that the seminar report titled 'Viral symbionts of parasitoids' has been completed by me independently after going through the reference cited here and I haven't copied from any of the fellow students or previous seminar reports.

Vellanikkara  
25/01/2020

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## **CERTIFICATE**

This is to certify that the seminar report entitled ‘Viral symbionts of parasitoids’ has been solely prepared by Abinsha Ashraf (2018-11-033) under my guidance and has not been copied from fellow students.

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## 1. Introduction

Insects are chronically colonized by microorganisms that are not overtly pathogenic and are often beneficial or even required by the insect host. Most of the cells in a healthy insect are microbial, and the microbiota accounts for up to 1–10% of the insect's biomass. As a result, an insect is fundamentally a multiorganismal entity. Microbiota constitute bacteria, archaea, fungi and viruses. Among this, Viruses are considered to be the least studied ones. Viruses of insects can be both beneficial and harmful ones. Entomopathogenic viruses are the ones which causes diseases in insects and there are numerous virus which can be beneficial to insects too.

<b>Virus group</b>	<b>Hosts</b>	<b>Beneficial effect</b>
Polydnviruses	Parasitoid wasps	Required for survival of the wasp egg in its insect host
Retroviruses	Mammals	Involved in the evolution of the placenta
Pararetroviruses	Plants	Protect against pathogenic viruses
Herpesviruses	Humans	Suppress HIV infection
Parvoviruses	Aphids	Required for the development of wings
Phages	Bacteria	Allow the invasion of new territory by killing off competitors
Yeast viruses	Fungi	Allow the suppression of competitors
Fungal viruses	Fungi and plants	Confer thermal tolerance to fungal endophytes and their plant hosts
Plant viruses	Plants	Confer drought and cold tolerance

Insect parasitoids are quantitatively and qualitatively important components of terrestrial ecosystems in terms of biodiversity and ecological impact. Most parasitoids are hymenopterans, with smaller numbers of dipteran and coleopteran species. They lay their eggs on or in other insects that serve as hosts for their offspring. Parasitoids are well known as members of the third trophic level, but many are members of even higher trophic levels, exploiting other parasitoids as hosts for their progeny. Juvenile

endoparasitoids develop in intimate association with their host. They are exposed to their host's physiology and immune system. Just like any other animal, insect parasitoids host a community of symbiotic microbes, including viruses, bacteria, and fungi. These symbionts and their effects on parasitoid ecology are attracting rapidly increasing attention. Parasitoid wasps have evolved various intricate symbiotic associations with viruses, most of which are mutualists. Parasitoid-associated viruses are well known to suppress host immunity, thus promoting successful development of the parasitoid in its host (Strand and Burke, 2014). However, recent studies have shown that parasitoid symbionts may influence host phenotype more extensively. This influence results in far-reaching ecological effects that extend well beyond interactions between the parasitoid and its host. For instance, upon injection of parasitoid-associated symbionts into their hosts, the microbes may influence interactions between the host and its food plant, thereby influencing the plant phenotype with consequences for plant immunity, interactions between the plant and herbivores, parasitoids that attack the herbivores, and hyperparasitoids that attack the parasitoids. Thus, parasitoid-associated symbionts influence direct interactions as well as indirect, plant-mediated interactions between organisms associated with the food plant of the parasitoid's host at different trophic levels. This means that microbial symbionts of parasitoids may influence the phenotype of the parasitoid in unprecedented ways, making them an impressive example of the extended phenotype.

## **2. Diversity of viral symbionts**

A wide variety of viruses have been reported as symbionts of parasitoid wasps, representing double-stranded DNA viruses (Ascoviridae, Polydnaviridae, Entomopoxviridae), single-stranded RNA viruses (Coronaviridae, Iflaviridae, Rhabdoviridae), and segmented double-stranded RNA viruses (Reoviridae). Among the viral families, Polydnaviridae is the major family of symbiotic viruses in insect.

## **3. Polydnaviridae**

Polydnaviridae are large, double-stranded DNA (dsDNA) viruses mainly associated with order Hymenoptera. PDV particles were first observed about 40 years ago, and the Polydnaviridae was recognized as a family by the International Committee on Taxonomy of Viruses in 1991. All PDV-carrying wasps belong to a superfamily named



Ichneumonoidea, which consists of two families, the Braconidae and Ichneumonidae, that diverged approximately 150 million years ago. The Polydnviridae is also currently divided into two genera named the Bracovirus and Ichnovirus. Bracoviruses (BVs) are associated with an estimated 50,000 species of braconids in six subfamilies. Ichnoviruses (IVs) are associated with approximately 14,000 species of ichneumonids in two subfamilies.

Each PDV persists as an integrated provirus in the germ line and somatic cells of every individual of a given wasp species. As such, PDVs are endogenous virus elements (EVEs) that have become genetically fixed in different wasp lineages. Unlike other known EVEs of ancient origin, however, PDVs retain the ability to replicate, which occurs only in female wasps in the nuclei of calyx cells that are located in the reproductive system. Replication begins during the mid-pupal phase and usually continues during adulthood. The virions that assemble in calyx cells contain multiple circular dsDNAs that are non equimolar in abundance and have large aggregate sizes (190–730 kb). The name Polydnviridae derives from this feature, and the totality of DNA segments packaged into virions during replication is referred to as the encapsidated form of the genome. Once assembled, virions are released from calyx cells and stored in the lumen of the oviducts with mature wasp eggs (Figure 1).

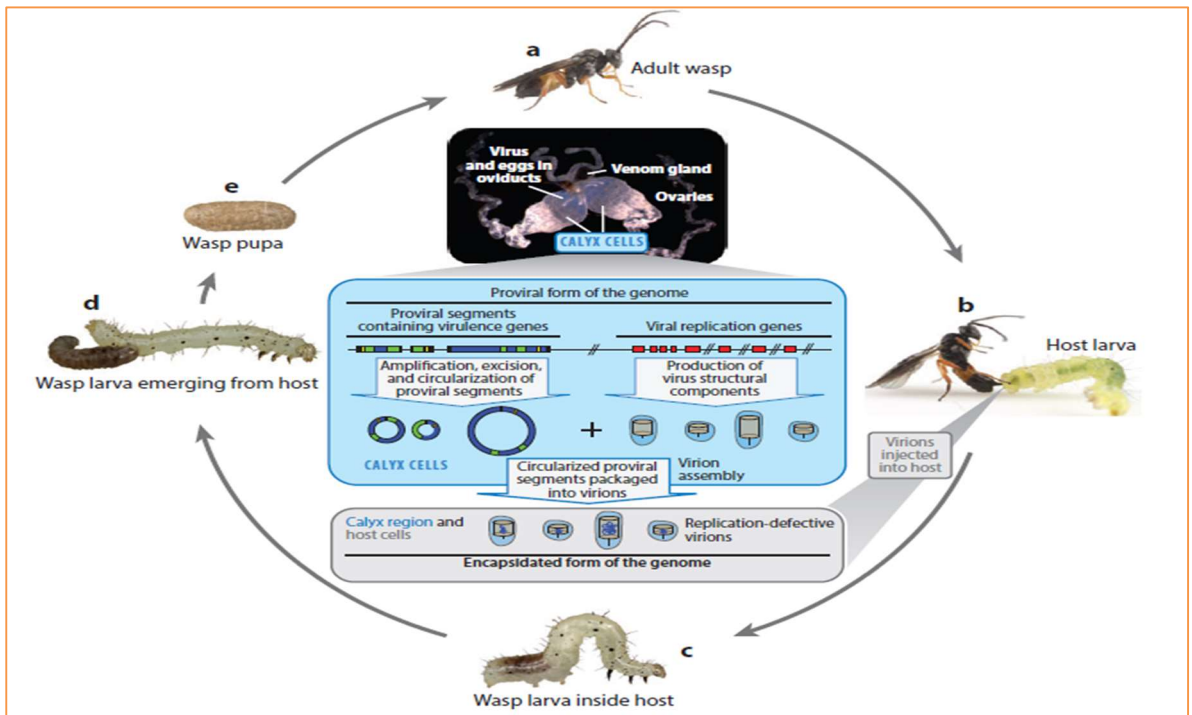


Fig.1 Lifecycle of PDV

#### **4. Localisation and Transmission of viral symbionts**

PDVs are produced in specific cells localized in the calyx region of the ovary and venom glands (Strand and Burke, 2013). Parasitoid-associated symbionts can be transmitted vertically or horizontally. Horizontal transmission are mainly seen in superparasitism.

#### **5. Effect of viral symbionts**

Viral symbionts show their effect on parasitoids, parasitized host and also on plant mediated multitrophic levels. In parasitoid, it is by manipulating its reproduction and also help in the survival of their offspring. Whereas in parasitized host, symbionts can manipulating host behavior, modify competitive ability and also promote interspecific parasitoid facilitation.

#### **6. Effect of symbionts on parasitoids**

##### **6.1. Manipulation of parasitoid reproduction**

Viruses associated with parasitoids can manipulate was preproduction. In *Leptopilina boucardi*, a double-stranded DNA virus named LbFV is capable of vertical and horizontal transmission and manipulates the oviposition behavior of the parasitoid by inducing superparasitism in infected females. Superparasitism favors horizontal transmission when uninfected and infected females lay eggs in the same host. As *L. boucardi* is a solitary parasitoid, implying that a host can sustain the development of only a single parasitoid, this behavior is not adaptive for the wasp and can also have negative consequences for population dynamics and interspecific competition (Varaldi *et al.*, 2003).

##### **6.2. Survival of parasitoid offspring**

Parasitoids that lay eggs in the body of living hosts need to suppress their immune response to develop successfully. The most common host immune response is the encapsulation of parasitoid eggs, a process in which the parasitoid egg is enveloped by a layer of hemocytes, leading to its death. PDVs have been extensively documented as mutualistic viral symbionts associated with braconids and ichneumonids, protecting parasitoid eggs by preventing encapsulation. In addition to PDVs, other parasitoid-associated viruses (ascoviruses, reoviruses, entomopoxviruses) and VLPs provide

similar protection. For example, the *Diachasmimorpha longicaudata* entomopoxvirus (DIEPV) occurs in the venom apparatus of female *D. longicaudata* wasps and is introduced into *Anastrepha suspense* fly larvae during parasitism. The virus replicates both in the wasp and in the fruit fly host, where it inhibits encapsulation, thus allowing the successful development of parasitoid offspring (Lawrence, 2005).

## **7. Effect of symbionts in parasitized hosts**

### **7.1. Manipulating Host Behavior**

A fascinating aspect of parasitoid–symbiont ecology is that the symbiont may manipulate the behavior of the parasitoid’s host. In the model system comprising *Dinocampus coccinellae* (hymenopteran parasitoid) and *Coleomegilla maculata* (coccinellid host), the host displays zombie-like paralytic behavior, which protects the parasitoid offspring (Figure 2). Interestingly, the behavioral manipulation occurs after the parasitoid larva has egressed from the host. An RNA virus of the parasitoid *D. coccinellae*, *D. coccinellae* paralysis virus (DcPV), that has remained in the host after parasitoid egression is most likely involved in this process. DcPV particles are located in the oviduct of *D. coccinellae* females and replicate within the parasitoid larvae as well as in their coccinellid hosts. In particular, DcPV replication in the coccinellid’s brain induces neuropile alterations that correlate with the paralytic symptoms typical of the behavioral manipulation. After clearance of the virus, normal coccinellid behavior is restored, suggesting that changes in lady beetle behavior are the result of manipulation by the parasitoid-associated virus rather than by the activity of the parasitoid itself (Dheilly *et al.* , 2015).

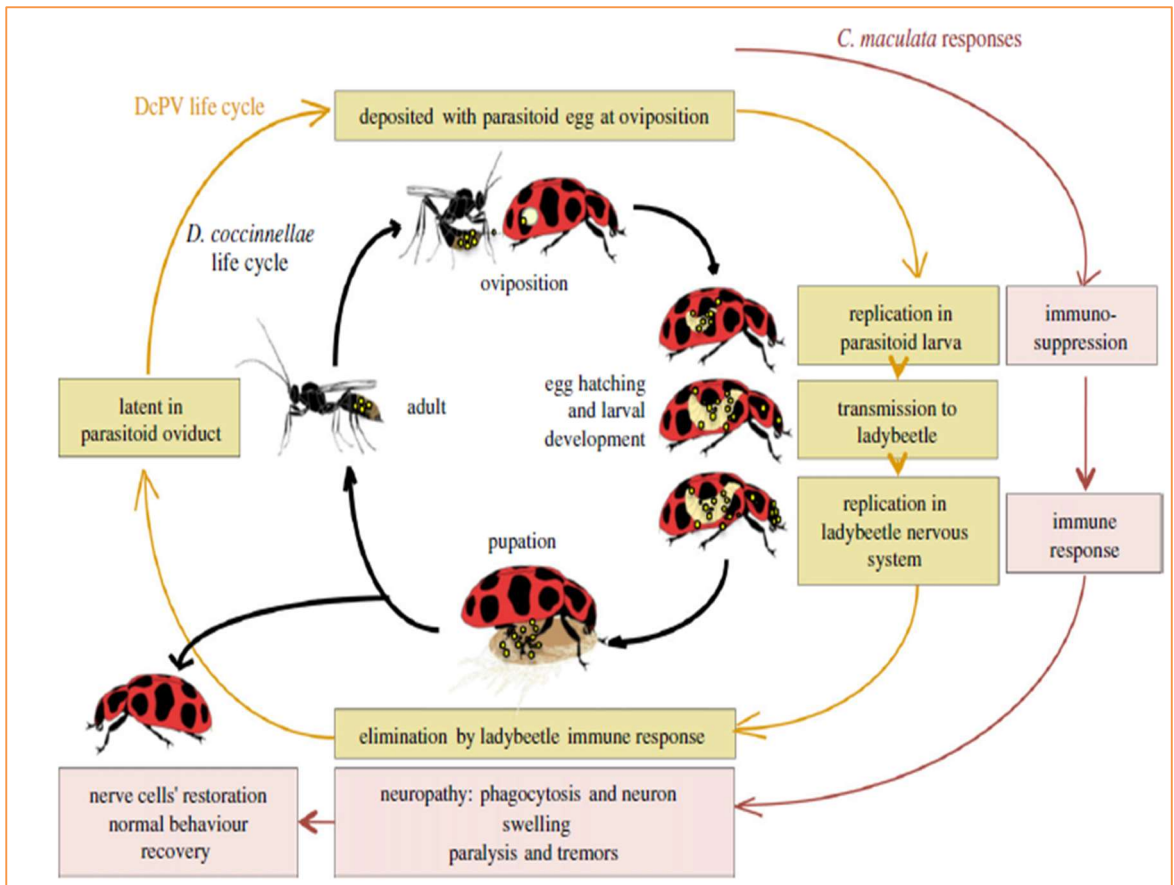


Fig. 2 Zombie bodyguard behaviour

### 7.2. Modifying Competitive Abilities

An interesting case of symbiont-mediated interspecific competition has been documented for two congeneric *Leptopilina* parasitoids that naturally coexist in the field (73). Under controlled laboratory conditions, *L. boulardi* outcompeted *Leptopilina heterotoma* in the absence of LbFV, whereas the parasitoid species coexisted when *L. boulardi* was infected by LbFV. As the viral symbiont induces superparasitism and egg wastage in *L. boulardi*, the resulting reduced host exploitation abilities allow the coexistence of the inferior competitor *L. heterotoma* (Patot *et al.* , 2012).

### 7.3. Promoting Interspecific Parasitoid Facilitation

Finally, parasitoid-associated symbionts may also promote interspecific facilitation when a parasitoid species benefits from interspecific competition. This may occur when a parasitoid species that is a superior competitor in larval competition interacts with another species that is better at suppressing host defenses with the aid of a symbiont. Because PDVs play a major role in disrupting host immunity, these parasitoid-associated symbionts may mediate interspecific facilitation. Although no competitive experiments were carried out, Vinson & Stoltz showed that *Campoletis sonorensis* eggs developed better in the host *Trichoplusia ni* when injected together with *Hyposoter exiguae* PDVs than with *C. sonorensis* PDVs.

## 8. Symbionts and plant-mediated multitrophic interactions

The ecological importance of microbial symbiosis in insects is well recognized for herbivore associated microorganisms in, for example, expansion of herbivore food-plant range, detoxification of plant defensive chemicals by herbivores, and protection against natural enemies of herbivores. Microorganisms in herbivores thus affect the strength of trophic relationships and insect community organization. Several recent studies have shown that parasitoid-associated symbionts may also directly or indirectly affect multitrophic interactions and community organization.

Injection of parasitoid-associated symbionts such as PDVs into the host during parasitization may alter herbivore traits as well as plant responses to herbivory and may subsequently affect the direction and strength of plant interactions with other organisms. Plants may respond differentially to attack by parasitized versus unparasitized caterpillars and aphids. These responses result in altered interactions of the plant with herbivores, parasitoids, and hyperparasitoids. Direct evidence that these interactions are caused by PDVs and not by the parasitoid larvae comes from manipulative studies in two very different plant–herbivore–parasitoid tritrophic relationships. Injection of PDVs of *Microplitis croceipes* (McBV) into *Helicoverpa zea* caterpillars affects tomato plant quality and benefits the performance of parasitoid larvae growing in caterpillars that feed on the induced plant. Injection of *C. glomerata* PDV (CgBV) and the parasitoid's venom, which catalyzes PDV activity, into

caterpillars of *P. brassicae* feeding on cabbage plants affects subsequent colonization of the plant by the diamondback moth (*Plutella xylostella*) as well as attraction of hyperparasitoid enemies of *Cotesia*. PDVs directly target the salivary glands of the caterpillars, and in both study systems the PDVs influenced the activity of enzymes in the caterpillar salivary glands. PDV-altered activity of the enzymes glucose oxidase and  $\beta$ -glucosidase may have elicited the plant response to parasitized caterpillars. However, direct induction of plant responses by the PDVs cannot yet be excluded. A transcriptome analysis of *P. brassicae* caterpillar salivary glands revealed the expression of viral genes; thus, viral proteins may come into direct contact with damaged plant tissue through the oral secretions of the caterpillar (Tan *et al.* , 2018).

Parasitoid-mediated induction of plant responses has been shown to change the plant's phenotype with consequences for plant-mediated interactions between early (*Pieris brassicae*) and subsequent (*Plutella xylostella*) herbivore colonisers: for example the moth *P. xylostella* prefers to oviposit on cabbage plants previously infested with unparasitised *P. brassicae* caterpillars compared to plants infested with caterpillars parasitised by *Cotesia glomerata*. Such parasitoid-mediated induction of plant responses occurs via phenotypic changes in the herbivore's oral secretions (regurgitant and/or saliva) which are known to play a key role in inducing plant defence responses; indeed, many elicitors that plants use to counteract herbivore attack have been identified in the oral secretions of caterpillars that come in contact with plant tissues during herbivore feeding. Isolated parasitoid eggs, venom and calyx fluid (containing PDV particles) from the gregarious parasitoid *Cotesia glomerata* and injected these parasitoid-derived components into secondinstar *P. brassicae* caterpillars subsequently feeding on wild *Brassica oleracea* plants.

Diamondback moths preferred to oviposit on *B. oleracea* leaves induced by PBS-injected *P. brassicae* caterpillars over leaves induced by caterpillars simultaneously injected with PDVs+venom, isolated from the parasitoid *C. glomerata*. Diamondback moths have been suggested to selectively oviposit on plants previously attacked by unparasitised *P. brassicae* caterpillars because their progeny suffers lower mortality due to reduced larval parasitism in the presence of *P. brassicae* caterpillars. Localization of host plants by diamondback moths may be based on volatile organic compounds specific for brassicaceous host plants (i.e. glucosinolate-breakdown

products), which are released in high amounts in response to herbivory by unparasitised *P. brassicae* caterpillars. After herbivory by *P. brassicae*, diamondback moths can detect plant phenotypic changes caused by BoMYR, which codes for myrosinase, an enzyme important for the metabolism of glucosinolate-breakdown products. Diamondback moths adjust their oviposition preferences based on plant phenotypic changes induced by oral secretions of *P. brassicae* caterpillars simultaneously injected with PDVs and venom. In contrast, changes in quantitative plant traits due to differences in the amount of damage inflicted by differentially injected caterpillars did not affect diamondback moth oviposition discrimination. The key role of herbivore salivary secretions is also supported by evidence that surgical removal of labial salivary glands from *P. brassicae* disrupts oviposition preference of diamondback moths. In fact, plants previously attacked by *P. brassicae* caterpillars with ablated salivary glands are perceived by diamondback moths as undamaged control plants, regardless of the parasitism status of the caterpillars. Due to the importance of salivary glands, it is possible that plant phenotypic changes which affect colonisation by diamondback moths are triggered by changes in elicitors induced by injection of PDVs and venom in *P. brassicae* caterpillars. Indeed, PDVs target several tissues when injected into caterpillars and salivary glands are also specifically infected suggesting a direct effect of PDVs on salivary secretions (Cusumano *et al.* , 2018).

## 9. Dynamic interactions between viruses

Complicated interactions among multiple viruses can result in host immunity suppression and allow for the development of the parasitoid offspring. The reovirus DpRV1 replicates in the ichneumonid wasp *D. pulchellus*, but it has no apparent impact on the wasp's fitness. This virus is transmitted to pupae of the lepidopteran host *A. assectella*, where it does not replicate but still has a subtle effect. In the lepidopteran host, DpRV1 interacts with the associated ascovirus DpAV4, which is naturally coinjected during oviposition by *D. pulchellus*. When DpAV4 was experimentally injected into the lepidopteran host, infection occurred very rapidly, leading to early death of the host . However, replication of DpAV4 is much slower in natural parasitism events, suggesting that DpRV1 may contribute to the development of *D. pulchellus* by regulating the replication of DpAV4. Another RNA virus packaged within DpRV1 particles has been hypothesized to play a role in this process, highlighting the

complexity of these interactions. There may be other cases of multiple interactions among viruses, parasitoids, and the parasitoids' hosts, but the complexity of these systems has limited our understanding so far (Renault *et al.*, 2005).

## **10. Future perspectives**

Studies have centered around the suppression of host immune response and manipulation of host development, which allow parasitoid offspring to develop successfully. Other symbionts, such as Wolbachia bacteria or the virus LbFV, modify their wasp host's reproduction or behavior exclusively for their own benefit. Parasitoid endosymbionts that support their host's nutrition seem to be rare, likely because of the carnivorous nature of the parasitoid larvae. Other areas of future studies include persistence of symbionts in host, role of symbionts in hyperparasitism and use of viral symbionts in pest control.

## **11. Conclusion**

In spite of the common perception of viruses as pathogens, many viruses are in fact beneficial to their hosts in various ways. It is likely that many more examples of mutualistic viruses will be discovered in the coming years and can act as a potential agent in pest management.

## **12. Discussion**

**Q 1.** Do this symbiotic virus also interact with other microorganism inhabiting on insects?

Yes, the viral symbionts can interact with other microbes like bacteria and bacteria inhabiting in the insects. For eg, the interaction of LbFV and Wolbachia in drosophila larvae. Here, LbFV induce superparasitism parasitoids and Wolbachia confer protection to the host by inducing encapsulation of parasitoid eggs. So the parasitoid get protected from encapsulation as more number of eggs are laid in superparasitism. But the interaction is not direct as the virus is present in the parasitoid and bacteria is present in the host.

**Q 2.** Do the viral symbionts can be pathogenic to parasitoids?

The chance of viral symbionts can be pathogenic is extremely less because there is a hypothesis that the genome of parasitoid are derived from the genome of the viral



symbionts. So the chance of viral symbionts becoming pathogenic to parasitoids are extremely less.

**Q 3.** Are viral symbionts have any beneficial effect in humans?

There are reports that herpes virus have a beneficial effect on humans. Herpes virus can suppress the HIV infection in humans

**Q 4.** Is any viral symbionts commercially available?

No, commercial production of viral symbionts are in development stages only

**Q 5.** How the parasitoid get benefit from increase in plant nutrition?

Parasitoids are benefited by the increase in the nutrient status of plant. A caterpillar feeding on the nutrient rich plant will be healthier. So that, the parasitoid will be parasitizing on a nutrient rich host.

**Q 6.** How viral symbionts are influencing the subsequent attack of DBM on *P. brassicae* fed plants?

The herbivory by the *P. brassicae* caterpillar can induce the production of an enzyme myrosinase in the plant, which is important for the metabolism of glucosinolate-breakdown products. The glucosinolates are the compounds which attract DBM to crucifers. But when viral symbionts are associated with the parasitoids of *P. brassicae*, the virus will have an influence on the salivary glands and thereby, myrosinase are not produced in the plants. So that glucosinolates will not be produced and DBM will not be attracted to the plant in turn. So it proves the involvement of viral symbionts in mediating the interaction between insect community.

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**Abstract:**

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Admission no. : 2018-11-033

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Major Advisor: Dr. Berin Pathrose

Time : 09.15 am

**Viral symbionts of parasitoids**

**Abstract**

Viruses have been largely viewed as pathogens of plants and animals. Though the pathogenic nature of the viruses cannot be denied, there are many viruses inhabiting as symbiotic partners influencing health of their host. Some viruses are essential for survival of their host and some others give them a fighting chance in the competitive world of nature. One such group of beneficial viruses is the viral symbionts of parasitoids which are found to enhance the biocontrol potential of parasitoids. A vast majority of viral symbionts in parasitoids belong to the family Polydnaviridae (PDVs), that too associated only with hymenopteran superfamily Ichneumonoidea.

Viral symbionts can benefit the parasitoids by exerting a direct influence on parasitoid and their host as well as through plant mediated multitrophic interactions. The viral symbionts can manipulate the reproduction of parasitoid wasps. *Leptopilina bouvardi*, a solitary parasitoid on the larvae of *Drosophila melanogaster*, harbours a double-stranded DNA virus, *Leptopilina bouvardi* filamentous virus (LbFV), which manipulates the oviposition behaviour of the parasitoid by inducing superparasitism in the infected females (Varaldi *et al.*, 2003). Similarly, the mutualistic viral symbionts associated with the parasitoids protect the parasitoid eggs inside the host larvae by preventing encapsulation which is a defense mechanism by host (Lawrence, 2005).

Behaviour of the coccinellid host *Coleomegilla maculata* can be manipulated by the RNA virus, *Dinocampus coccinellae* paralysis virus (DcPV), present in the parasitoid *D. coccinellae*. The parasitized host protects the parasitoid pupae by

displaying a zombie-like paralytic behaviour, which will be revived after complete development of parasitoid (Dheilly *et al.*, 2015). The presence of the symbiotic virus LbFV facilitate the co-existence of *Leptopilina heterotoma* with the superior parasitoid *L. boulardi* (Patot *et al.*, 2012).

Role of parasitoid inhabiting symbionts in multitrophic interactions and community organization is also well known. Injection of PDVs of *Microplitis croceipes* bracovirus (McBV) into *Helicoverpa zea* caterpillars feeding on tomato was found to lower the production of defensive components by the plant, resulting in healthier host larvae (Tan *et al.*, 2018). Symbiotic viruses can interact with other viruses present in the same host and exert influence on the host. *Diadromus pulchellus*, a pupal parasitoid of *Acrolepiopsis assectella*, harbours *Diadromus pulchellus* ascovirus (DpAV4) and *D. pulchellus* reovirus (DpRV1). The symbiotic virus DpRV1 can contribute to the development of *D. pulchellus* by regulating the replication of DpAV4, which is pathogenic to the host (Renault *et al.*, 2005).

As can be seen, symbiotic viruses can enhance the performance of parasitoid in more ways than one. Such associations offer exciting possibilities in pest management in future, as our understanding about the interactions progresses.

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