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Impact of parasitoid-associated polydnaviruses on plant-mediated herbivore interactions

Erik H Poelman¹ and Antonino Cusumano²

Insect herbivores interact via plant-mediated interactions in which one herbivore species induces changes in plant quality that affects the performance of a second phytophagous insect that shares the food plant. These interactions are often asymmetric due to specificity in induced plant responses to herbivore attack, amount of plant damage, elicitors in herbivore saliva and plant organ damaged by herbivores. Parasitoids and their symbiotic polydnaviruses alter herbivore physiology and behaviour and may influence how plants respond to parasitized herbivores. We argue that these phenomena affect plant-mediated interactions between herbivores. We identify that the extended phenotype of parasitoid polydnaviruses is an important knowledge gap in interaction networks of insect communities.

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Introduction

Insect herbivores sharing a food plant often interact indirectly through plant-mediated effects [1–3]. Plant-mediated interactions occur when one herbivore species induces changes in plant morphology, defence chemistry or nutrition that affects the performance of a second phytophagous insect that is feeding on other plant organs or occupies the plant at a different time [1,2]. Although predators are predominantly considered to directly affect herbivore interactions by preying on herbivores [4], predators and parasitoids may also affect the outcome of plant-mediated interactions among herbivores through non-consumptive interactions [5,6,7••]. With their

presence, predators cause changes in herbivore behaviour such as shifts in the feeding intensity and feeding position of herbivores [7••,8,9]. Parasitoids that use phytophagous insects as hosts for their offspring even manipulate host physiology and behaviour that result in altered interactions of the phytophagous host with the food plant [10–15]. In the past decade, it has been identified that the induced plant responses by parasitized herbivores affect the performance of other herbivores feeding on the plant [16,17], food plant preference of herbivores [18,19••], as well as responses of parasitoids and hyperparasitoids to plant volatiles [11,20]. Recently, functional analyses of the mechanisms underlying the plant-mediated interactions initiated by parasitoids identified that not the larvae of the parasitoid, but the parasitoid associated polydnaviruses (PDVs) that are injected into the caterpillar host along with the parasitoid egg are the key drivers of the interaction network [19••,21••,22,23].

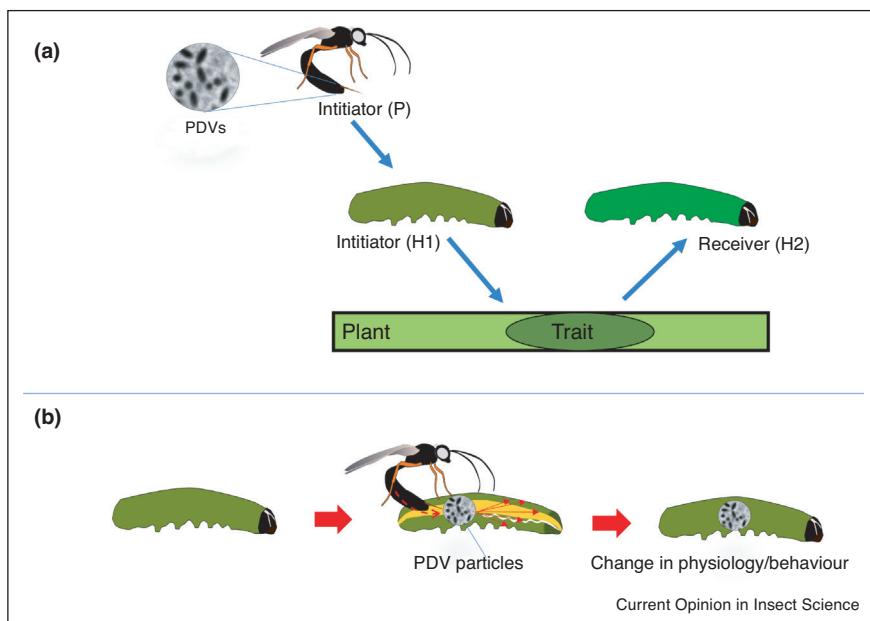
Here we argue that parasitoid-associated polydnaviruses have an impact on plant-mediated interactions among insect herbivores by altering insect host physiology and behaviour (Figure 1). We illustrate how PDVs may influence interactions beyond host manipulation, discuss whether these effects are adaptive to the parasitoid and provide evidence for a key role of PDVs in altering plant-mediated interactions among herbivores. Although parasitism of aphids affects plant responses [17], aphid associated parasitoids do not have a symbiosis with PDVs. We therefore focus our review on PDVs and caterpillar associated parasitoids.

How do PDVs affect plant responses to herbivore attack?

Although PDVs have long been described as viruses allowing the parasitoid offspring to escape the immune response of herbivore hosts [24•,25], it is now increasingly evident that PDVs also interact with the food plant of the herbivore [19••,21••,22,23,26]. One question that remains to be explored is whether PDVs actively manipulate plant responses to herbivory, or instead the effects that PDVs induce on plants are simply a by-product of the action that PDVs exert on the infected herbivore.

An evidence in favour of the ‘active manipulation hypothesis’ is that PDV-induced plant-mediated effects enhance the fitness of the parasitoid larva growing inside the parasitized caterpillar [19••,21••]. Indeed, plants have been shown to reduce their chemical defences when attacked by herbivores experimentally injected with

Figure 1



Impact of PDVs on plant-mediated interactions between two herbivores.

(a) Insect herbivores indirectly interact via plant-mediated interactions in which one herbivore species (initiator H1) induces changes in plant traits that affects the performance of a second phytophagous insect (receiver H2) that shares the food plant. Parasitoids and their symbiotic polydnaviruses (PDVs) can also act as initiators (P) by inducing phenotypic changes in herbivores that alter the interaction network. **(b)** PDV particles injected by parasitoid females into a caterpillar host infect several tissues (including salivary glands and the gut) which eventually alter herbivore physiology and behaviour (drawing based on scheme by Utsumi *et al.* [7^{**}]).

PDV particles, which in turn likely increased the nutritional quality of the host food plant for the parasitized herbivore [19^{**},21^{**}]. This outcome is mediated by the effect that PDVs induce on the caterpillar oral secretions which often contain elicitors that the plants use to recognize the identity of the herbivore attacker [27,28]. Once PDV particles are delivered in the herbivore hemocoel, they infect several tissues among which salivary glands can be targeted [22,29]. PDVs impact the composition of caterpillar salivary glands via quantitative effects leading to a reduction of the activity of caterpillar-resident elicitors (i.e. beta-glucosidase and glucose oxidase) [21^{**},22] as well as qualitative effects resulting in the production of viral-encoded peptides [23]. The recent discovery of viral 'alien' proteins (GlyPro1_Hd2, GlyPro2_Hd2) in salivary glands of infected herbivores opens new lines of research to investigate their possible role at the plant-insect interface.

Alternatively, PDV-induced effects on plants may be a by-product of the complex effects that PDVs induce in the infected caterpillar: the fundamental functions of PDVs are to suppress the host immunity and regulate the caterpillar metabolism in order to allow the successful development of the parasitoid progeny inside the

herbivore host [24[•],25]. Concerning the latter, PDVs exert a wide range of effects on the caterpillar which experiences inhibition of protein synthesis [30,31], disruption of hormone balance [32–39], developmental arrest [35,37,40], inhibition of growth [41–45] and prevention of metamorphosis [46]. Because the herbivore phenotype is extensively affected after PDV infection, one may argue that such alterations subsequently affect the interactions that the herbivore establishes with its food plant. An evidence supporting the by-product hypothesis is that plant-mediated PDV-induced responses are not always beneficial to the parasitoid and can result in increased mortality by its hyperparasitoid enemies [22]. Yet the ecological costs of PDVs due to plant-mediated effects are probably minor when compared to the benefit conferred by PDVs to their parasitoid partners via herbivore-mediated effects.

While it is challenging to disentangle the active versus passive effects of PDVs in plant-insect interactions, there is clear evidence showing that PDVs truly alter plant phenotypic responses to herbivory [19^{**},21^{**},22, 23,26]. As a result, PDVs can also act as hidden players affecting indirect plant-mediated interactions among herbivores.

Parasitoids and their PDVs affect plant-mediated interactions between herbivores

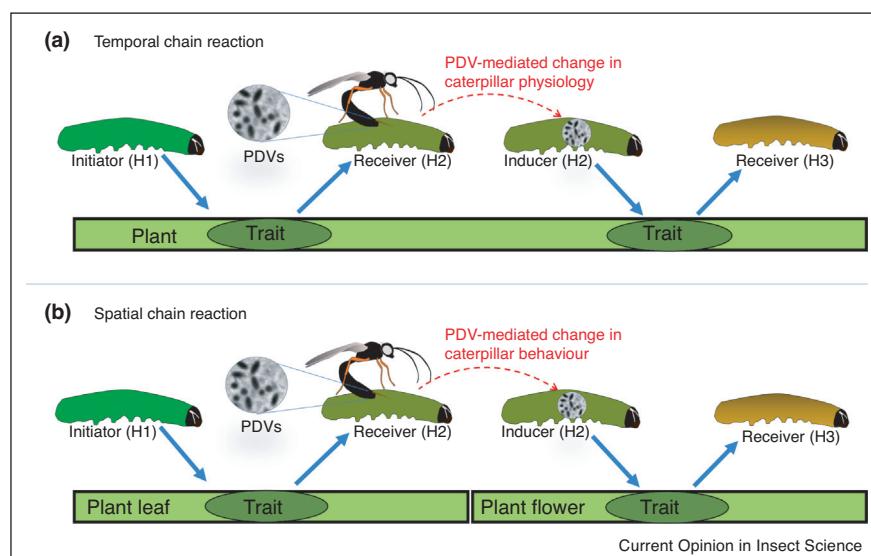
Plant-mediated interactions between herbivores are often asymmetric due to specificity in plant induced responses to herbivores and herbivore adaptations to plant defences [2,47]. Plant responses to insect feeding are specific for the phytophagous insect that is feeding on the plant, because herbivores differ in the mode of feeding (leaf chewing or phloem feeding), the amount and pattern of damage they cause, the plant organ they feed on as well as the composition of elicitors in oral secretions that trigger an induced plant response [2,3]. Moreover, herbivore species differ in how they are affected by plant responses such as their resistance or tolerance to morphological and chemical defences and the plant tissue they feed on [47]. Since parasitoids and their PDVs alter how plants respond to feeding by their herbivore host, this may lead to an important route of how parasitoids affect plant-mediated interactions among herbivores (Figure 2).

Physiological changes in herbivores

In regulating the host metabolism for the benefit of the parasitoid offspring, PDVs may affect the development and nutritional needs of the host. Many solitary parasitoids and their associated PDVs reduce the host development to fewer instar stages, which is associated with

reduced plant damage [16]. For example, when PDVs isolated from the solitary wasp *Hyposoter didymator* are injected in *Spodoptera frugiperda* caterpillars, a reduction of feeding damage is observed on corn leaves, compared with uninfected caterpillars [23]. Some gregarious parasitoids have been found to extend the host development with increased plant damage or even with an additional more ferociously feeding instar stage [48]. Such quantitative variation in plant damage by parasitized and PDV-infected herbivores may correspond with the magnitude of induced plant responses that affect subsequent herbivores feeding from the plant [16]. Parasitism of *Pieris rapae* by the solitary parasitoid *Cotesia rubecula* reduced plant damage compared to unparasitized caterpillars and resulted in similar performance of a second generation of unparasitized *P. rapae* caterpillars feeding on parasitized caterpillar induced plants compared to undamaged plants [16]. However, the congeneric gregarious parasitoid *Cotesia glomerata* slightly increased feeding by its host and reduced performance of a second generation of *P. rapae* feeding on induced plants. Because in this host-parasitoid system *C. glomerata* bracoviruses (CgBV) have been identified to be key regulators of the host [49] and these specific PDVs affect plant induced responses [19^{••},22], we may speculate that PDVs were responsible for the differential plant-mediated effects on performance of a second generation of *P. rapae*. For the two genera of PDVs, bracoviruses (BVs) and ichnoviruses (IVs), plant

Figure 2



Impact of PDVs on plant-mediated interaction networks.

(a) PDVs can control for the amount of feeding time and damage inflicted to plants by parasitized caterpillars. This phenotypic change in infected caterpillars further modulates the way the herbivore induces plant traits causing temporal effects in the interaction network. (b) PDVs can induce non-consumptive effects in parasitized caterpillars altering the movement patterns of the herbivore on the plant. This phenotypic change in infected caterpillars further modulates the way the herbivore induces plant traits causing spatial effects in the interaction network. H1, H2 and H3 indicate different herbivore species (drawing based on scheme by Utsumi *et al.* [7[•]]).

induction by PDV-injected caterpillars leads to effects on subsequent performance of the herbivore host [21^{••},23]. In pepper plants parasitism of aphids attenuated the enhanced performance of thrips feeding on plants previously attacked by unparasitized aphids [17]. This example in aphid parasitoids that do not carry PDVs illustrates that parasitoids may affect plant-mediated interactions among different herbivore species, even though these interactions may also be neutral [50]. Whether PDVs are responsible for parasitoid effects on plant-mediated herbivore interactions is still largely unexplored. The potential of interspecific plant-mediated interactions initiated by PDVs is established for herbivore preference. The diamondback moth *Plutella xylostella* prefers to lay eggs on cabbage leaves that have been previously induced by unparasitized *Pieris* caterpillars over leaves induced by *Pieris* caterpillars carrying PDV-associated parasitoids. By controlling for the amount of plant damage using a pattern wheel and applying oral secretions of parasitized and unparasitized *Pieris* caterpillars, it has become evident that parasitoids affect the plant-mediated interaction through qualitative changes in herbivore oral secretions [18]. Microinjection of PDVs separate from the parasitoid eggs, yielded evidence that indeed the PDVs were driving these effects [19^{••}].

The mechanisms by which PDVs may affect induced plant responses and thereby plant-mediated interactions among herbivores may involve a complex interplay of microorganisms. Recent studies on parasitoids carrying PDVs identify that parasitisation alters the host microbiome [51] with organ specific changes such as the composition of the gut microbiome [52[•]]. We speculate that PDVs may also alter the microbiome of herbivore oral secretions and thereby affect induced plant responses. This includes a role for the microbiome of the salivary gland and the foregut that is regurgitated by some herbivores on the plant during feeding [53]. Similar to how Colorado potato beetles use microorganisms to suppress plant responses to their feeding [54], PDVs may alter food plant quality through changes in caterpillar microbiome for the benefit of the parasitoid offspring. Since specificity in induced plant responses is leading to asymmetry in plant-mediated interactions among herbivores, we argue that PDVs may directly or indirectly affect – through herbivore physiology – plant-mediated herbivore interactions.

Behavioural changes in herbivores

In addition to herbivore physiology, PDVs may alter herbivore behaviour [10,55,56]. Changes in herbivore behaviour, such as their feeding position on the plant or the feeding duration by for example relocation to neighbouring plants affects patterns of induced plant response and thus plant-mediated interactions among herbivores [3,7^{••}].

Usurpation of herbivore behaviour by parasitoids is widespread. Many parasitoids that parasitize aphids or caterpillars manipulate the movement of their herbivore host just before parasitoid pupation [56]. The parasitoid directs the herbivore to a position where the parasitoid pupa is less conspicuous to its predatory and hyperparasitic enemies [57–59]. Usurpation of herbivore movement may establish itself early in host development to reduce exposure of the parasitized caterpillar to predators. Alteration in movement patterns will cause changes in feeding duration, distribution of damage across a plant and the specific position where the herbivore feeds. These quantitative aspects of herbivore damage to plants have been found to affect plant induced responses to herbivory and contributes to variation in plant-mediated herbivore interactions [3,7^{••}]. Parasitoid-associated viruses have been shown to be involved in usurpation of host movement. For example, when the coccinellid *Coleomegilla maculata* is parasitized by the endoparasitoid *Dinocampus coccinellae*, it displays – after parasitoid egression – a ‘zombie-behaviour’ that protects the wasp larvae from predators. This host manipulation has been shown to correlate with infection in the coccinellid brain by the *D. coccinellae* paralysis virus (DcPV) which has remained inside the host after parasitoid egression [60]. A similar zombie-behaviour occurs in *Pieris brassicae* caterpillars when attacked by the wasp *C. glomerata*, and it would be interesting to investigate if *C. glomerata* bracovirus (CgBV) is involved in such host manipulation. Thus the changes that parasitoids and their associated viruses induce on the movement patterns of herbivores may generate spatial effects in the plant-mediated interaction network [7^{••}].

A few studies identified intricate qualitative changes in feeding behaviour by parasitized herbivores that are likely to affect plant-mediated herbivore interactions, although in these studies the parasitoids are not associated with PDVs. Parasitoids of gall midges affect the shape and size of gall formation in plants, likely to enhance the protection that the gall offers to the parasitoid against its hyperparasitoid enemies [12]. The induction of gall formation is an apparent form of a change in plant quality and is likely to result in plant-mediated effects on performance of other herbivores feeding on the gall itself or leaves on which galls have formed. Parasitoids of aphids have been found to alter feeding of their aphid host from phloem to xylem. Such markedly different plant tissues being damaged by parasitized herbivores is likely to affect other herbivores feeding from the same plant via plant-mediated interactions [61]. We hypothesize that PDVs in caterpillar associated parasitoids may affect plant-mediated interactions through similar changes in feeding behaviour of caterpillars as found for parasitoids not carrying PDVs.

Although we lack causal evidence that these effects of parasitoids on behaviour of their herbivore host can be directly attributed to PDVs, evidence of these extended effects of viruses is found in Baculoviruses, which are closely related to Bracoviruses. Baculoviruses in caterpillars interfere with Protein tyrosine phosphatase (PTP) activity of the host and cause hyper-active and abnormal herbivore movement [62–64]. The *ptp* genes are widely represented in Bracoviruses and these PDVs are thus likely to cause the behavioural manipulation of the host in similar ways as Baculoviruses.

Future perspective

Current evidence for PDVs affecting plant-mediated interactions among herbivores is indirect and arises when bringing together different fields of research such as PDV host usurpation and induction of plant responses by parasitized herbivores. Nevertheless, the extended phenotype of parasitoid associated PDVs on plant quality and the fact that each parasitoid species is associated with its own specific symbiotic virus, suggest that PDVs contribute to variation in plant-mediated interactions among herbivores. Future studies should explore whether parasitoids and their PDVs developing in one herbivore species affect the performance of other herbivore species sharing the food plant. These studies should deepen functional understanding of the mechanisms by which PDVs interact with the host and food plant. Drawing parallels with host manipulation by Baculoviruses will stimulate the functional understanding of PDV — host interactions. This will be especially beneficial for Bracoviruses whereas the yet unknown origin of Ichnoviruses makes this group of PDVs particularly challenging to characterize from a functional perspective [65]. Interaction networks in insect communities induced by PDVs are also likely to extend to interactions among higher trophic level organisms such as connecting parasitoids that develop inside different herbivores feeding on other plant organs or that occupy the plant at a different time [16]. To understand evolution of host manipulation by PDVs in parasitoids, we should include the costs and benefits of PDVs interacting directly and indirectly with the food plant of their herbivore host. Moreover, the extended phenotype of PDVs on the food plant may cascade to plant-mediated effects across trophic levels and impact common interaction networks that are unexplored in insect community ecology [66].

Conflict of interest statement

Nothing declared.

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