

1 **Impact of parasitoid-associated polydnaviruses on plant-mediated herbivore**
2 **interactions**

3 **Short title: PDVs affect plant-mediated herbivore interactions**

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13

14 **Abstract**

15 Insect herbivores interact via plant-mediated interactions in which one herbivore species
16 induces changes in plant quality that affects the performance of a second phytophagous insect
17 that shares the food plant. These interactions are asymmetric by variation in induced plant
18 responses to herbivores caused by feeding mode, amount of damage, elicitors in herbivore
19 saliva and plant organ damaged by herbivores. Parasitoids and their symbiotic polydnaviruses
20 alter herbivore physiology and behaviour and thereby influence how plants respond to
21 parasitized herbivores. We argue that these phenomena affect plant-mediated interactions
22 between herbivores. We identify that the extended phenotype of parasitoid polydnaviruses is
23 an important knowledge gap in interaction networks of insect communities.

24

25 **Keywords:** parasitoid microbes; extended phenotype; plant-insect-microbe interactions, trait-
26 mediated indirect interactions, plant-mediated interaction networks

27

28 **Introduction**

29 Competition among insect herbivores sharing a food plant is prevalent through plant-mediated
30 interactions (1-3). Plant-mediated interactions occur when one herbivore species induces
31 changes in plant morphology, defence chemistry or nutrition that affects the performance of a
32 second phytophagous insect that is feeding on other plant organs or occupies the plant at a
33 different time (1,2).

34 In addition to directly dampening competitive interactions by preying on herbivores
35 (4), predators and parasitoids may also affect the outcome of plant-mediated interactions
36 among herbivores (5-7). With their presence, predators create a landscape of fear that causes
37 changes in herbivore behaviour such as shifts in the intensity of feeding and feeding position
38 of herbivores (7-9). Parasitoids that use phytophagous insects as host for their offspring even
39 manipulate host physiology and behaviour that results in altered interactions of the
40 phytophagous host with the food plant (10-15). In the past decade, it has been identified that
41 the induced plant responses by parasitized herbivores affect the performance of other
42 herbivores feeding on the plant (16,17), food plant preference of herbivores (18,19), as well as
43 responses of parasitoids and hyperparasitoids to plant volatiles (11, 20). Recently, functional
44 analyses of the mechanisms underlying the plant-mediated interactions initiated by parasitoids
45 identified that not the larvae of the parasitoid, but the parasitoid associated polydnnaviruses
46 (PDVs) that are injected into the caterpillar host along with the parasitoid egg are the key
47 drivers of the interaction network (19, 21-23).

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

56

57 **Why do PDVs affect plant responses to herbivore attack?**

58 Although PDVs have long been described as viruses allowing the parasitoid offspring to
59 escape the immune response of herbivore hosts (24, 25), it is now increasingly evident that
60 PDVs also interact with the food plant of the herbivore (19, 21-23,26). One question that

61 remains to be explored is whether PVDs actively manipulate plant responses to herbivory, or
62 instead the effects that PDVs induce on plants are simply a by-product of the action that
63 PDVs exert on the infected herbivore.

64 An evidence in favour of the “active manipulation hypothesis” is that PDV-induced plant-
65 mediated effects enhance the fitness of the parasitoid larva growing inside the parasitized
66 caterpillar (19, 21). Indeed, plants have been shown to reduce their chemical defences when
67 attacked by herbivores experimentally injected with PDV particles, which in turn likely
68 increased the nutritional quality of the host food plant for the parasitized herbivore (19, 21).
69 This outcome is mediated by the effect that PDVs induce on the caterpillar oral sections
70 which often contain elicitors that the plants use to recognize the identity of the herbivore
71 attacker (27, 28). Once PDV particles are delivered in the herbivore hemocoel, they infect
72 several tissues among which salivary glands are specifically targeted (22, 29). PDVs impact
73 the composition of caterpillar salivary glands via quantitative effects leading to a reduction of
74 the activity of caterpillar-resident elicitors (i.e. beta-glucosidase and glucose oxidase) (21, 22)
75 as well as qualitative effects resulting in the production of viral-encoded peptides (23). The
76 recent discovery of viral “alien” proteins (GlyPro1_Hd2, GlyPro2_Hd2) in salivary glands of
77 infected herbivores opens new lines of research to investigate their possible role at the plant-
78 insect interface.

79 Alternatively, PDV-induced effects on plants may be a by-product of the complex effects that
80 PDVs induce in the infected caterpillar: the fundamental functions of PDVs are to suppress
81 the host immunity and regulate the caterpillar metabolism in order to allow the successful
82 development of the parasitoid progeny inside the herbivore host (24, 25). To achieve this,
83 PDVs exert a wide range of effects on the caterpillar which experiences inhibition of protein
84 synthesis (30, 31), disruption of hormone balance (32-39), developmental arrest (35, 37, 40),
85 inhibition of growth (41-45) and prevention of metamorphosis (46). Because the herbivore
86 phenotype is extensively affected after PDV infection, one may argue that such alterations
87 subsequently affect the interactions that the herbivore establishes with its food plant. An
88 evidence supporting the by-product hypothesis is that plant-mediated PDV-induced responses
89 are not always beneficial to the parasitoid and can result in increased mortality by its
90 hyperparasitoid enemies (22). Yet the ecological costs of PDVs due to plant-mediated effects
91 are probably minor when compared to the benefit conferred by PDVs to their parasitoid
92 partners via herbivore-mediated effects.

93 While it is challenging to disentangle the active versus passive effects of PDVs in plant-insect
94 interactions, there is clear evidence showing that PDVs truly alter plant phenotypic responses
95 to herbivory (19, 21- 23, 26). As a result, PDVs can also act as hidden players affecting
96 indirect plant-mediated interactions among herbivores.

97

98 **Parasitoid and their PDVs affect plant-mediated interactions between herbivores**

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

110 *Physiological changes in herbivores*

111 In regulating the host metabolism for the benefit of the parasitoid offspring, PDVs may affect
112 the development and nutritional needs of the host. Many solitary parasitoids and their
113 associated PDVs reduce the host development to fewer instar stages, which is associated with
114 reduced plant damage (16). For example, when PDVs isolated from the solitary wasp
115 *Hyposoter didymator* are injected in *Spodoptera frugiperda* caterpillars, a reduction of
116 feeding damage is observed on corn leaves, compared with uninfected caterpillars (23). Some
117 gregarious parasitoids have been found to extend the host development with increased plant
118 damage or even with an additional more ferociously feeding instar stage (48). Such
119 quantitative variation in plant damage by parasitized and PDV-infected herbivores may
120 correspond with magnitude of induced plant responses that affect subsequent herbivores
121 feeding from the plant (16). Parasitism of *Pieris rapae* by the solitary parasitoid *C. rubecula*
122 reduced plant damage compared to unparasitized caterpillars and resulted in similar
123 performance of a second generation of unparasitized *P. rapae* caterpillars feeding on
124 parasitized caterpillar induced plants compared to undamaged plants (16). However, the

125 gregarious parasitoid *C. glomerata* slightly increased feeding by its host and reduced
126 performance of a second generation of *P. rapae* feeding on induced plants. Because in this
127 host-parasitoid system *Cotesia glomerata* bracoviruses (CgBV) have been identified to be key
128 regulators of the host (49) and these specific PDVs affect plant induced responses (19, 22), we
129 may speculate that PDVs were responsible for the differential plant-mediated effects on
130 performance of a second generation of *P. rapae*. For the two genera of PDVs, bracoviruses
131 (BV) and ichnoviruses (IV), plant induction by PDV-injected caterpillars leads to effects on
132 subsequent performance of the herbivore host (21, 23). In pepper plants parasitism of aphids
133 attenuated the enhanced performance of thrips feeding on plants previously attacked by
134 unparasitized aphids (17). This example in aphid parasitoids that do not carry PDVs illustrates
135 that parasitoids may affect plant-mediated interactions among different herbivore species,
136 even though these interactions may also be neutral (50). Whether PDVs are responsible for
137 parasitoid effects on plant-mediated herbivore interactions is still largely unexplored. The
138 potential of interspecific plant-mediated interactions initiated by PDVs is established for
139 herbivore preference. Parasitoids of *Pieris* caterpillars affect egg deposition preference of
140 *Plutella xylostella* for herbivore induced plants. By controlling for the amount of plant
141 damage using a pattern wheel and applying oral secretions of parasitized and unparasitized
142 *Pieris* caterpillars, it has become evident that parasitoids affect the plant-mediated interaction
143 through qualitative changes in herbivore oral secretions (18). Microinjection of PDVs
144 separate from the parasitoid eggs, yielded evidence that indeed the PDVs were driving these
145 effects (19).

146 The mechanisms by which PDVs may affect induced plant responses and thereby
147 plant-mediated interactions among herbivores may be a complex interplay of microorganisms.
148 Recent studies on parasitoids carrying PDVs identify that parasitisation alters the host
149 microbiome (51) with organ specific changes such as the composition of the gut microbiome
150 (52). We speculate that PDVs may also alter the microbiome of herbivore oral secretions and
151 thereby affect induced plant responses. This includes a role for the microbiome of the salivary
152 gland and the foregut that is regurgitated by some herbivores on the plant during feeding (53).
153 Similar to how Colorado potato beetles use microorganisms to suppress plant responses to
154 their feeding (54), PDVs may alter food plant quality through changes in caterpillar
155 microbiome for the benefit of the parasitoid offspring. Since specificity in induced plant
156 responses is leading to asymmetry in plant-mediated interactions among herbivores, we argue

157 that PDVs may directly or indirectly affect - through herbivore physiology - plant-mediated
158 herbivore interactions.

159

160 *Behavioural changes in herbivores*

161 In addition to herbivore physiology, PDVs may alter herbivore behaviour (10, 55, 56).

162 Changes in herbivore behaviour, such as their feeding position on the plant or the feeding
163 duration by for example relocation to neighbouring plants affects patterns of induced plant
164 response and thus plant-mediated interactions among herbivores (3, 7).

165 Usurpation of herbivore behaviour by parasitoids is widespread. Many parasitoids that
166 parasitize aphids or caterpillars manipulate the movement of their herbivore host just before
167 parasitoid pupation (56). The parasitoid directs the herbivore to a position where the
168 parasitoid pupa is less conspicuous to its predatory and hyperparasitic enemies (57-59).
169 Usurpation of herbivore movement may establish itself early in host development to reduce
170 exposure of the parasitized caterpillar to predators. Alteration in movement patterns will cause
171 changes in feeding duration, distribution of damage across a plant and the specific position
172 where the herbivore feeds. These quantitative aspects of herbivore damage to plants have
173 been found to affect plant induced responses to herbivory and contributes to variation in
174 plant-mediated herbivore interactions (3, 7). Parasitoid-associated viruses have been shown to
175 be involved in usurpation of host movement. For example, when the coccinellid *Coleomegilla*
176 *maculata* is parasitized by the endoparasitoid *Dinocampus coccinellae*, it displays - after
177 parasitoid egression - a “zombie-behaviour” that protects the wasp larvae from predators. This
178 host manipulation has been shown to correlate with infection in the coccinellid brain by the *D.*
179 *coccinellae* paralysis virus (DcPV) which has remained inside the host after parasitoid
180 egression (60). A similar zombie-behaviour occurs in *Pieris brassicae* caterpillars when
181 attacked by the wasp *Cotesia glomerata*, and it would be interesting to investigate if *C.*
182 *glomerata* bracovirus (CgBV) is involved in such host manipulation. Thus the effects of
183 parasitoids and their associated viruses on movement patterns of herbivores spatially connects
184 networks of plant-mediated interactions in plant stands (7).

185 A few studies identified intricate qualitative changes in feeding behaviour by
186 parasitized herbivores that are likely to affect plant-mediated herbivore interactions, although
187 in these studies the parasitoids are not associated with PDVs. Parasitoids of gall midges affect
188 the shape and size of gall formation in plants, likely to enhance the protection that the gall

189 offers to the parasitoid against its hyperparasitoid enemies (12). The induction of gall
190 formation is an apparent form of a change in plant quality and is likely to result in plant-
191 mediated effects on performance of other herbivores feeding on the gall itself or leaves on
192 which galls have formed. Parasitoids of aphids have been found to alter feeding of their aphid
193 host from phloem to xylem. Such markedly different plant tissues being damaged by
194 parasitized herbivores is likely to affect other herbivores feeding from the same plant via
195 plant-mediated interactions (61).

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

203

204 **Future perspective**

205 Current evidence for PDVs affecting plant-mediated interactions among herbivores is indirect
206 and arises when bringing together different fields of research such as PDV host usurpation
207 and induction of plant responses by parasitized herbivores. Nevertheless, the extended
208 phenotype of parasitoid associated PDVs on plant quality and the fact that each parasitoid
209 species is associated with its own specific symbiotic virus, suggest that PDVs contribute to
210 variation in plant-mediated interactions among herbivores. Future studies should explore
211 whether parasitoids and their PDVs developing in one herbivore species affect the
212 performance of other herbivore species sharing the food plant. These studies should deepen
213 functional understanding of the mechanisms by which PDVs interact with the host and food
214 plant. Drawing parallels with host manipulation by Baculoviruses will stimulate the functional
215 understanding of Bracovirus - host interactions. The yet unknown origin of Ichnoviruses
216 instead makes this group of PDVs particularly challenging to characterize from a functional
217 perspective (65). Interaction networks in insect communities induced by PDVs are also likely
218 to extend to interactions among higher trophic level organisms such as connecting parasitoids
219 that develop inside different herbivores feeding on other plant organs or that occupy the plant
220 at a different time (16). To understand evolution of host manipulation by PDVs in parasitoids,

221 we should include the costs and benefits of PDVs interacting directly and indirectly with the
222 food plant of their herbivore host. Moreover, the extended phenotype of PDVs on the food
223 plant may cascade to plant-mediated effects across trophic levels and represent common
224 interaction networks that are unexplored in insect community ecology (66).

225

226 **Figure1. Impact of PDVs on plant-mediated interactions between two herbivores. (A)**
 227 Insect herbivores indirectly interact via plant-mediated interactions in which one herbivore
 228 species (initiator H1) induces changes in plant traits that affects the performance of a second
 229 phytophagous insect (receiver H2) that shares the food plant. Parasitoids and their symbiotic
 230 polydnaviruses (PDVs) can also act as initiators (P) by inducing phenotypic changes in
 231 herbivores that alter the interaction network. **(B)** PDV particles injected by parasitoid females
 232 into a caterpillar host infect several tissues (including salivary glands and the gut) which
 233 eventually alter herbivore physiology and behaviour (drawing based on scheme by Utsumi et
 234 al. 2010).

235

Fig. 1A

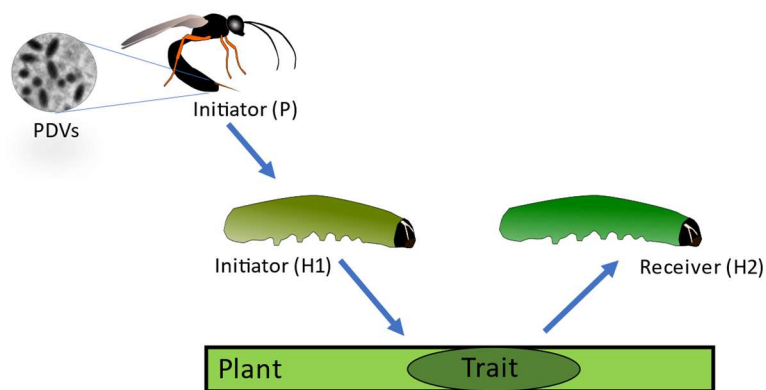
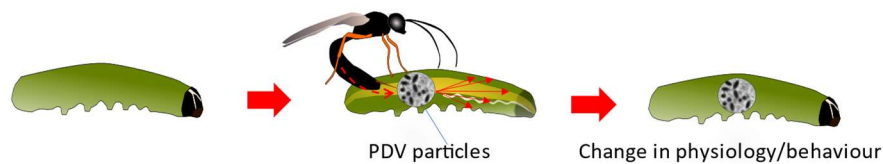


Fig. 1B



236

237

238 **Figure 2. Impact of PVDs on plant-mediated interaction networks.** (A) PDVs can control
 239 for the amount of feeding time and damage inflicted to plants by parasitized caterpillars. This
 240 phenotypic change in infected caterpillars further modulates the way the herbivore induces
 241 plant traits causing temporal effects in the interaction network. (B) PDVs can induce non-
 242 consumptive effects in parasitized caterpillars altering the movement patterns of the herbivore
 243 on the plant. This phenotypic change in infected caterpillars further modulates the way the
 244 herbivore induces plant traits causing spatial effects in the interaction network. H1, H2 and
 245 H3 indicate different herbivore species (drawing based on scheme by Utsumi et al. 2010).

Fig. 2A Temporal chain reaction

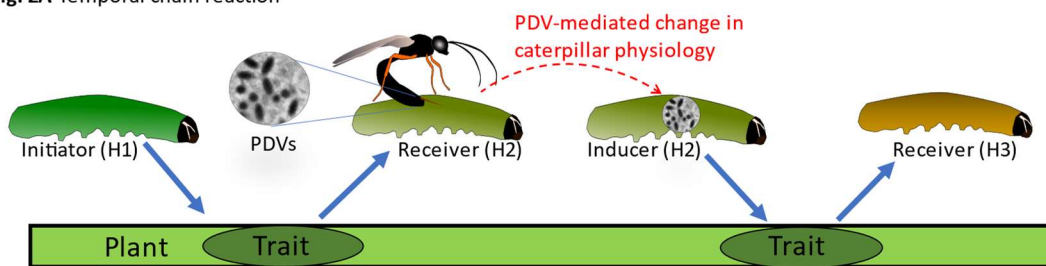
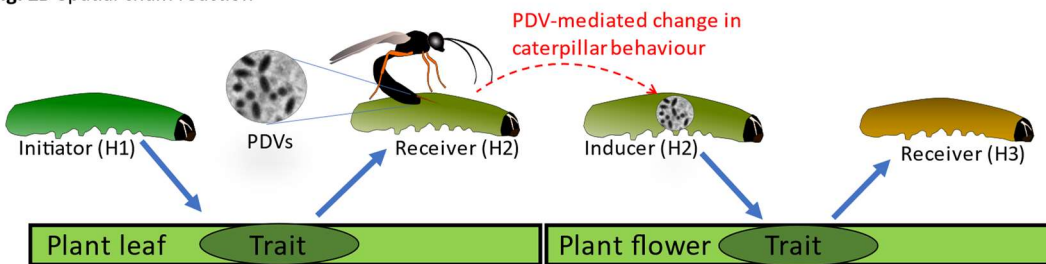


Fig. 2B Spatial chain reaction



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254

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