

Parasitoids affect plant responses through their host *Pieris brassicae*, but not for the benefit of their own performance

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Abstract

1. Upon parasitism, many parasitoids inject symbiotic viruses and venom into their host. Thereby, they modify the hosts physiology including its saliva composition and, in turn, plant perception of herbivory.
2. It has been hypothesised that parasitoids manipulate plant responses to increase their host performance and maximise their own fitness. However, it is still unclear whether parasitoids are under selective pressure to increase plant quality or whether indirect changes in plants due to parasitism are a by-product of the physiological changes induced in their host.
3. We tested whether the parasitoids *Hyposoter ebeninus* and *Cotesia glomerata* manipulate induced plant responses through the host *Pieris brassicae* caterpillars to increase their own performance. During their entire lifespan, parasitised herbivores were fed with leaf material of *Brassica oleracea* plants that were left untreated or continuously exposed to feeding by either unparasitised, conspecific or heterospecific parasitised caterpillars. We measured the development time, weight, clutch size and mortality of parasitoids that emerged from caterpillars as proxy for their performance.
4. Both parasitoid species did not perform significantly better when their host was fed with leaves from plants continuously induced by a conspecific parasitoid relative to unparasitised caterpillars. However, parasitoid species asymmetrically affected each other's performance through plant-mediated interactions.
5. Our results do not support the hypothesis of parasitoids manipulating plant responses for their own benefit, suggesting that indirect plant-mediated interactions among parasitoids may be a by-product of host manipulation. However, our work confirms the significance of parasitoid-induced plant-mediated interactions in insect communities that to date are still understudied.

KEYWORDS

Brassica oleracea, *Cotesia glomerata*, host regulation, *Hyposoter ebeninus*, parasitoid performance, plant-mediated interactions

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INTRODUCTION

Plants have a wide array of defensive strategies against herbivore attacks. Among them, induced responses are specifically triggered by both herbivore mechanical damage and herbivore saliva composition (Alborn et al., 1997; Lin & Felton, 2020; Mattiacci & Dicke, 1995). Therefore, alteration of herbivore behaviour or saliva composition could, in turn, alter herbivore-induced plant responses. Such herbivore alteration typically happens when herbivores are parasitised by parasitic wasps (also called ‘parasitoids’) that attack herbivorous insects (Forbes et al., 2018; Vinson & Iwantsch, 1980).

Parasitoids typically lay one (solitary) or several (gregarious) eggs in their herbivorous host which can often still feed on plants during the parasitoid larval development (koinobiont parasitoids) (Godfray, 1994). Along with eggs, adult parasitoids inject several factors in their host, such as polydnviruses (PDVs) and/or venom (Asgari & Rivers, 2011; Rotherham, 1967). PDVs can be divided into two genera: Bracoviruses and Ichnoviruses, which can be found in parasitoids from the Braconidae and Ichnumonidae families, respectively (Strand & Burke, 2015). Parasitoid PDVs can have a significant effect on the regulation of their host development (Beckage & Gelman, 2004; Cuny & Poelman, 2022; Vinson & Iwantsch, 1980), ranging from premature arrestment (Dorémus, 2014) to prolongation (Beckage et al., 1994; Doucet & Cusson, 1996). This alteration can, in turn, lead to a reduction or an increase of the amount of damage done to the plant (Cuny et al., 2021; Ode, 2006). Physiological changes in parasitised herbivores also include alterations of their gut microbial community (Gloder et al., 2021; Wang et al., 2021) and in their saliva composition, which contain herbivore-associated molecules used by the plant to recognise the attacker and respond specifically to the species of herbivore that is attacking the plant (Bonaventure, 2012; Felton & Tumlinson, 2008; Mithöfer & Boland, 2008).

So far, parasitoid alteration of elicitors in herbivore saliva has been observed in three parasitoid species: two braconids (Cusumano et al., 2018; Tan et al., 2018; Zhu et al., 2018) and one ichneumonid (Cusumano et al., 2021). Overall, plants induced by parasitised herbivores produce less volatile compounds (Fatouros et al., 2005; Kafle et al., 2020) and have a lower defence response against herbivory (Cusumano et al., 2018; Tan et al., 2018) than plants induced by unparasitised herbivores. This, in turn, has important consequences for the whole insect community interacting with the induced plants (Cusumano & Volkoff, 2021). For example, unparasitised herbivores feeding on plants induced by parasitised herbivores have a higher performance than when they feed on plants induced by unparasitised herbivores (Cusumano et al., 2021). In addition, the attractivity of subsequent adult herbivores is reduced when plants are induced by parasitised herbivores (Poelman et al., 2011). Finally, even parasitoid larvae developing in a herbivore can be indirectly affected by another parasitoid whose host previously fed on the same plant (Poelman et al., 2011).

It can be hypothesised that the reduced plant defence response due to herbivore parasitism is adaptive and may reduce the attraction to hyperparasitoids that kill parasitoids (Zhu et al., 2015). However, recent studies do not seem to support this hypothesis (Zhu et al., 2018). An alternative hypothesis is that changes in plant defence response due to

parasitism may directly benefit the performance of the host, which may, in turn, have a positive effect on the parasitoid's fitness (Tan et al., 2018). In other words, parasitoids could indirectly manipulate plant responses to herbivory for their own benefit, through physiological modifications in their herbivorous host. This idea received very little attention so far, as most of the past research in tritrophic interactions has looked into the effects of plants on other trophic levels (Kaplan et al., 2016; Poelman et al., 2011).

In our study, we hypothesised that if parasitoid plant manipulation is adaptive, parasitoids should realise a higher fitness on plants induced by a conspecific parasitoid compared to an unparasitised herbivore. To test this hypothesis, we measured several parameters associated with fitness in a solitary ichneumonid (*Hyposoter ebeninus*) and a gregarious braconid (*Cotesia glomerata*) parasitoid that had developed inside *Pieris brassicae* caterpillars feeding from *Brassica oleracea* plants exposed to a range of unparasitised and parasitised herbivore treatments. In addition, it is expected that plant-mediated interactions among heterospecific parasitoids will result in asymmetrical, unpredictable effects on parasitoid performance (Poelman et al., 2011; Tan et al., 2019). Therefore, to have more heterospecific comparisons among parasitoid species, we added the solitary parasitoid *Cotesia rubecula* as a plant inducer. The herbivorous hosts (*P. brassicae*) were fed during their entire lifespan with plants subjected to one among five herbivory treatments: (i) no herbivore (control), (ii) one unparasitised *P. brassicae*, (iii) one *P. brassicae* parasitised by *H. ebeninus*, (iv) one *P. brassicae* parasitised by *C. glomerata* and (v) one *P. brassicae* parasitised by *C. rubecula*. We discuss our results in the context of the evolution of tritrophic interactions among plants, herbivores and parasitoids.

MATERIALS AND METHODS

Plants

We used 5-week-old wild *B. oleracea* plants of which seeds were originally derived from Kimmeridge, Dorset, UK, 50°36'0"N, 2°07'0"W (Gols et al., 2008) and multiplied by open pollination in a field with multiple wild *B. oleracea* genotypes. This plant had been shown to respond differently to parasitised and unparasitised caterpillars (Zhu et al., 2015). Plants were grown in 2-L pots under greenhouse conditions (18–26°C, 50%–70% relative humidity), under natural daylight and SON-T light (500 $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$; L16:D8; Philips). They were fertilised three times per week and watered every other day.

Insects

The herbivore *P. brassicae* as well as two *Cotesia* parasitoids (*C. glomerata* and *C. rubecula*) were originally collected near Wageningen University, the Netherlands, while the parasitoid *H. ebeninus* was originally collected near the University of Rennes, France (Harvey et al., 2010). *C. glomerata* is a gregarious, haemolymph-feeding parasitoid, *C. rubecula* a solitary haemolymph feeder, while *H. ebeninus* is a solitary tissue-feeder (Gols

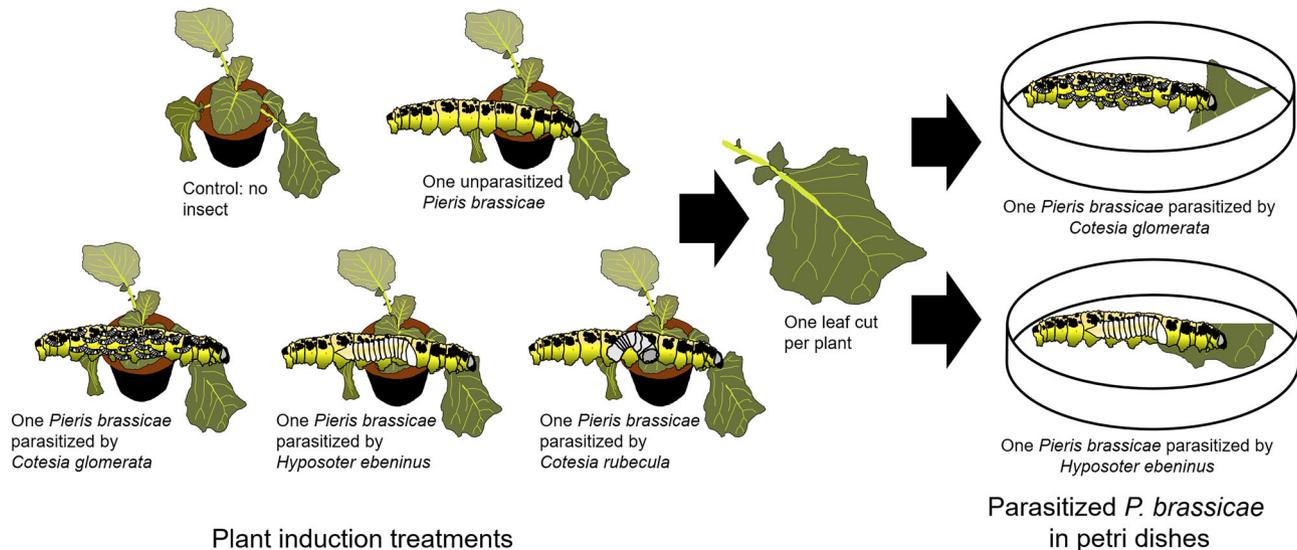


FIGURE 1 Schematic diagram of the experimental design, the five plant induction treatments and the performance of two parasitoid species (*Cotesia glomerata* and *Hyposoter ebeninus*) developing inside *Pieris brassicae* caterpillars feeding on the leaves of one of these five plant treatments in Petri dishes. Caterpillars were fed with leaf pieces until pupation and emerging parasitoids were dried and weighed.

et al., 2015; Harvey et al., 1999). The three parasitoid species use *P. brassicae* as a host, although *C. rubecula* is predominantly found on *P. rapae* in the Netherlands. All the insects used in this study were routinely reared at the Laboratory of Entomology, Wageningen University. *P. brassicae* was reared on cultivated cabbage plants (*B. oleracea*, variety: gemmifera cv. Cyrus) and the three parasitoids were reared on first instar *P. brassicae* caterpillars also fed with cultivated cabbage plants. To obtain parasitised caterpillars for our experiments, each caterpillar was individually parasitised by one of the three parasitoid species in Petri dish. A caterpillar was considered parasitised when the parasitoid had inserted its ovipositor for at least 5 s for *C. glomerata* and 1 s for *C. rubecula* and *H. ebeninus* (Poelman et al., 2014). We did not check for the success of the parasitism as previous work showed that 99% of the caterpillars parasitised had at least an egg inside (Poelman et al., 2011). However, it is possible that some eggs were encapsulated by the herbivore immune response. Nevertheless, the event of parasitism secured that all the caterpillars received venom and polydnavirus which are the main factors responsible for host physiological changes and induced plant responses by parasitised caterpillars (Zhu et al., 2018).

Experimental design

We tested the performance of two parasitoid species (*H. ebeninus* and *C. glomerata*) whose host (*P. brassicae*) was fed during its entire lifespan with leaves cut from plants (*B. oleracea*) induced by parasitised and unparasitised caterpillars. This experimental design (Figure 1) was required to prevent the tested parasitised caterpillars from newly induced leaves they feed on and thereby potentially manipulate leaf quality for its own benefit. Although this design allows the restriction of induction by only a single parasitised herbivore treatment, cutting leaves from the plant could have induced plant defensive compounds

as well. Because all the leaves and plants from each treatment were cut the same way, we assume that the only difference left among treatments is due to the continuous herbivory treatments on the plants.

Newly parasitised first instar *P. brassicae* (by either *C. glomerata* or *H. ebeninus*, depending on the experiment) were individually housed in Petri dishes (diameter: 5.5 cm) and fed with leaf pieces cut from one of five plant treatments: (i) no induction (control), (ii) one first instar unparasitised *P. brassicae*, or one first instar *P. brassicae* parasitised by one of the three following parasitoids: (iii) *C. glomerata*, (iv) *H. ebeninus* or (v) *C. rubecula*. Caterpillars were placed on a fully expanded leaf of each plant, inside a mesh bag and control plants received an empty mesh bag. After 2 days, the mesh bag and the caterpillar were moved to another leaf on the same plant. The leaf with 2 days of caterpillar feeding was cut at the base and used to feed parasitised caterpillars in Petri dishes. This was repeated every other day (or over the weekend) until adult parasitoid emergence. The same protocol was applied to undamaged control plants. One leaf was cut into 4–6 pieces that were used to feed parasitised larvae each housed in their own Petri dish. When plants were almost entirely defoliated (which could happen toward the very end of the experiments, especially in the case of *C. glomerata* which has a longer development time than *H. ebeninus*), a new plant was used according to the same protocol. Petri dishes were kept in an incubator (23°C, 16L:8D). In this study, we did not measure the differences in plant damage resulting from parasitism by different parasitoid species. Therefore, we cannot separate the quantitative (amount of damage) and qualitative (plant elicitors) aspects of herbivory that are affected by parasitoids and are responsible for plant-mediated interactions.

As a proxy for parasitoid performance, the following parameters were measured: (i) parasitoid mortality, (ii) development time from parasitism to parasitoid adult emergence, (iii) parasitoid adult dry

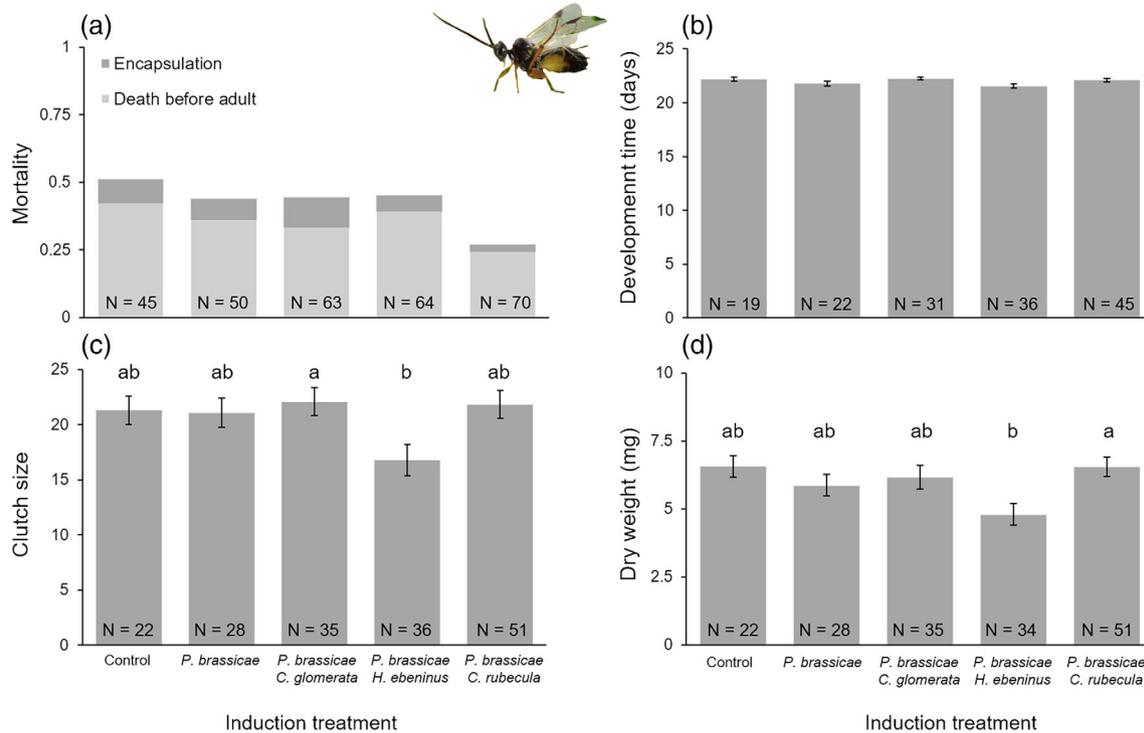


FIGURE 2 Mean mortality (a), development time from parasitism to parasitoid cocoon formation (b), number of emerged parasitoids (c) and adult dry weight (d) of *Cotesia glomerata* fed with leaf pieces from undamaged plants, plants damaged by unparasitised caterpillars, or plants damaged by parasitised caterpillars that host conspecific or heterospecific parasitoids. Different letters among treatments indicate statistically significant differences ($p < 0.05$). Bars indicate standard error of the mean.

weight (adults were dried in an oven at 80°C for 48 h) and we weighed each individual on a Sartorius®-CP2P-Analytical Balance (accuracy 0.001 mg) and (iv) number of adult parasitoids emerging per clutch (in the case of the gregarious parasitoid *C. glomerata*).

Because of a relatively low number of female *H. ebeninus* offspring, both sexes were analysed jointly. Both sexes were also analysed jointly for *C. glomerata* progeny, because of the cryptic difference and the time needed to sex thousands of individuals.

We conducted a first experiment with *P. brassicae* parasitised by *C. glomerata* in Petri dishes (one block with the following number of Petri dishes per treatment: control: 45, unparasitised: 50, *C. glomerata*: 63; *H. ebeninus*: 64 and *C. rubecula*: 70). A second experiment was performed with *H. ebeninus*-parasitised larvae as receiver in Petri dishes (three blocks with the following total of Petri dishes per treatment: control: 113, unparasitised: 113, *C. glomerata*: 132; *H. ebeninus*: 149 and *C. rubecula*: 146).

Statistical analyses

All analyses were performed with R (version 4.0.4, R Core Team 2021) using the lme4 package for mixed models. Linear mixed models were used for parasitoid development time and adult dry weight. Generalised linear mixed models were used for parasitoid mortality (binomial distribution), number of adult parasitoids emerging in the case of the gregarious parasitoid *C. glomerata* (Poisson distribution).

In all models, the plant induction treatments were included as fixed factor with the five treatment levels. In mixed models with *C. glomerata*, individual plants were used as random factors, because the host of several parasitoids received leaves from the same individual plant. For the same reason, we also used individual plants as random factors in mixed models with *H. ebeninus* but it was also nested in blocks, as the experiment with *H. ebeninus* was repeated three times.

RESULTS

Cotesia glomerata

Mortality and development time of the gregarious parasitoid *C. glomerata* was similar when developing in caterpillars that were fed with undamaged plants, or plants damaged with unparasitised, conspecific or heterospecific parasitised caterpillars (mortality: $\chi^2_{(4)} = 6.91$, $p = 0.14$; development time: $\chi^2_{(4)} = 8.34$, $p = 0.08$) (Figure 2). The relative number of parasitoids that emerged from the brood ($\chi^2_{(4)} = 10.1$, $p = 0.04$) as well as adult parasitoid dry mass ($\chi^2_{(4)} = 10.79$, $p = 0.029$) were affected by the treatments of plants that were fed to the caterpillar host. Although none of the treatments differed from caterpillars fed with undamaged control plants, relative number of emerged parasitoids was higher for *C. glomerata* whose host was fed with plants damaged by a heterospecific parasitoid (*H. ebeninus*) compared to plants damaged by conspecific

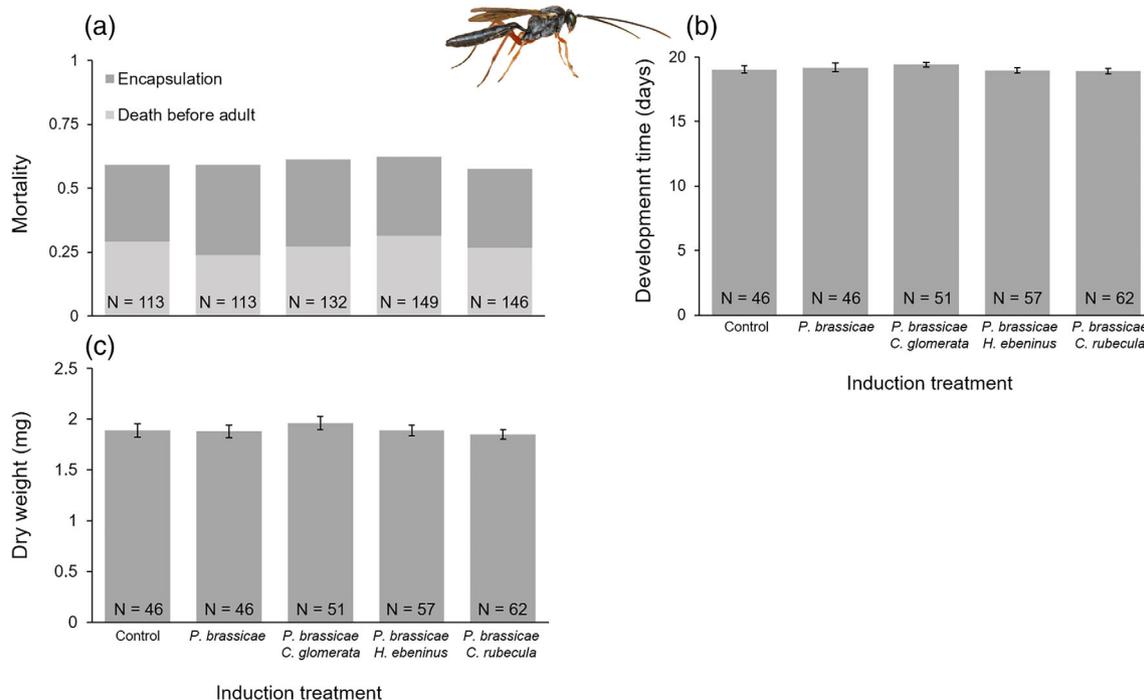


FIGURE 3 Mean mortality (either due to encapsulation by the host immune system or to the death of the parasitised larva) (a), development time from parasitism to parasitoid cocoon formation (b) and adult dry weight (c) of *Hyposoter ebeninus* parasitoids fed with leaf pieces from undamaged plants, plants damaged by unparasitised caterpillars, or plants damaged by parasitised caterpillars that host conspecific or heterospecific parasitoids. Bars indicate standard error of the mean.

parasitoids. Similarly, the mean dry weight of adult *C. glomerata* was significantly lower when their host was fed with plants damaged by a caterpillar parasitised by a heterospecific parasitoid (*H. ebeninus*), compared to plants damaged by a caterpillar parasitised by another heterospecific parasitoid (*C. rubecula*) (Figure 2).

Hyposoter ebeninus

The solitary parasitoid *H. ebeninus* was not affected by the food source of its host. None of the performance parameters differed for parasitoids that had developed in caterpillars fed with undamaged control leaves or those damaged by unparasitised, conspecific or heterospecific parasitised caterpillars (Figure 3). Plant induction treatments had no significant effect on mortality ($\chi^2_{(4)} = 0.86$, $p = 0.9$), development time ($\chi^2_{(4)} = 3.2$, $p = 0.53$) and adult dry weight ($\chi^2_{(4)} = 1.8$, $p = 0.77$) of *H. ebeninus*.

DISCUSSION

For two parasitoid species, we show that herbivore host feeding on plants induced by a conspecific parasitoid does not have a beneficial effect on parasitoid traits associated with fitness when compared to plants induced by unparasitised herbivores. Hence, our results do not support the hypothesis of parasitoids indirectly manipulate the

host plant response to herbivory for their own benefit. Yet, we found asymmetrical plant-mediated interactions among parasitoid species. The number of emerged *C. glomerata*, as well as their dry weight did not differ from control plants. However, fewer *C. glomerata* emerged when their host had been fed with leaves that were damaged by caterpillars hosting the solitary heterospecific parasitoid *H. ebeninus* than the numbers that emerged from caterpillars fed with leaves from plants induced by other con- and heterospecific parasitoids. In contrast, *H. ebeninus* was not affected by the induction treatments of the plants that their host was fed with. These results suggest that the identity of the parasitoid developing in a herbivore host is an important driver of plant-mediated interactions among insects.

According to our first hypothesis, if parasitoids are under natural selection to change plant responses to herbivory to increase their own fitness, we expect parasitoids to perform better when fed with plants induced by a conspecific parasitoid compared to plants induced by an unparasitised caterpillar. Evidence for this hypothesis was found for the braconid parasitoid *Microplitis croceipes* which performs better when its host is fed with leaves induced by saliva from caterpillars parasitised by a conspecific parasitoid compared to unparasitised ones (Tan et al., 2018). However, the opposite outcome was found when *M. croceipes* developed in another host/host-plant system (Tan et al., 2019). These contrasting results reveal that depending on the host and host-plant system, plant perception of parasitised herbivores does not always lead to positive effects on parasitoids. In this context, the present study furthers our

understanding of parasitoid putatively manipulating plant response to herbivory for their own fitness by testing the performance of two parasitoids fed with leaves from plants left intact or damaged by one unparasitised or parasitised caterpillar. This type of set-up allowed us to feed parasitised herbivores with leaves from plants that were continuously induced during the entire parasitoid lifespan. This is closer to a natural induction than the use of a single induction event with controlled leaf damage and herbivore saliva or a short time span of feeding by parasitised caterpillars used in previous studies (Cusumano et al., 2018, 2021; Tan et al., 2018, 2019). We did not find a significant effect of conspecific parasitoid plant induction relative to unparasitised hosts on any of the traits associated with fitness measured for the two parasitoids *C. glomerata* and *H. ebeninus*. One plausible explanation for our results is that koinobiont parasitoids altering plant perception of the herbivore could be a by-product of the considerable physiological changes observed in parasitised hosts (Beckage & Gelman, 2004; Vinson & Iwantsch, 1980). Consequently, these host modifications could sometimes lead to a lower plant response and a higher parasitoid fitness. Equally likely, parasitoids can also induce a stronger plant defensive response, which decreases their own performance (Ode et al., 2016; Tan et al., 2019). We may argue that parasitoid plant manipulation for their own benefit only takes place in systems where the amount of plant defensive compounds induced by the herbivorous host has an important negative impact on parasitoid fitness (Ode, 2006, 2019; Turlings & Benrey, 1998). Hence, the degree of specialisation of the parasitoid and its host to plant defence may play an important role in the outcome of parasitoid plant manipulation. Another alternative is that other parameters may maintain or favour the evolution of parasitoid plant manipulation. For example, parasitoid plant manipulation could be selected to reduce plant attraction to other organisms, such as competitive parasitoids or hyperparasitoids (Kafle et al., 2020; Zhu et al., 2018).

We found support for our second hypothesis of an asymmetrical plant-mediated effect among heterospecific parasitoids. While *H. ebeninus* parasitoids were not affected by induced plant responses to parasitised caterpillars hosting any of the three parasitoids, *C. glomerata* had a smaller brood size as well as a lower adult dry weight when the plants were induced by *H. ebeninus*-parasitised herbivores, compared with plants induced by herbivores parasitised by *C. glomerata* or *C. rubecula*, respectively. *C. glomerata* may be more susceptible to plant defensive compounds because its development time is longer than that of *H. ebeninus*. However, *H. ebeninus* should be more exposed to chemical compounds as it consumes its host entirely before pupation, while *C. glomerata* only feeds on haemolymph (Gols & Harvey, 2009). It could also be hypothesised that *C. glomerata* is more adapted to plant responses induced by braconid parasitoids compared to ichneumonids. These results highlight the importance of the identity of the parasitoid developing inside a feeding herbivore when investigating plant-mediated species interactions (Poelman et al., 2011; Zhu et al., 2015). Only one other study has tested plant-mediated interactions among parasitoids feeding on the same plant (Poelman et al., 2011). *C. glomerata* and *C. rubecula* affect each other's performance differentially when developing in *Pieris rapae* caterpillars on plants induced by a previous generation of parasitised *P. rapae* caterpillars.

CONCLUSION

The hypothesis of parasitoids manipulating plant response to herbivory contrasts with the general view of parasitoids described as plant bodyguards (Cuny et al., 2021; Kaplan et al., 2016). It is increasingly recognised that parasitoids play an important role in affecting plant responses to herbivory, until a point where it is not very clear who, between the herbivore, the parasitoid and even their microbial symbionts, is driving the profile of plant-induced responses to parasitised caterpillars (Dicke et al., 2020; Kaplan, 2012). Our results suggest that parasitoid changes in plant herbivore identity perception may, for many cases, be by-products of host regulation by parasitoids to secure their successful development rather than an adaptive strategy to manipulate plant quality for their own benefit. However, these results need to be confirmed by other studies using different tritrophic systems. Indirect plant-mediated interactions among parasitoids are likely to be widespread in natural environments, but they are still largely unexplored.

AUTHOR CONTRIBUTIONS

Erik H. Poelman, Mitchel E. Bourne and Maximilien A. C. Cuny designed the experiment. Maximilien A. C. Cuny and Mitchel E. Bourne collected the data. Maximilien A. C. Cuny analysed the data and wrote the first draft of the manuscript. Mitchel E. Bourne and Erik H. Poelman critically revised the manuscript several times.

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CONFLICTS OF INTEREST

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are available from the corresponding author upon reasonable request.

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