

# Indirect plant-mediated interactions between heterospecific parasitoids that develop in different caterpillar species

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## Research Article

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# Abstract

Koinobiont parasitoids induce physiological changes in their herbivorous hosts that affect how plants respond to herbivory. The signature of parasitoids on induced plant responses to feeding by parasitized herbivores indirectly impacts insect communities interacting with the plant. The effect may extend to parasitoids and cause indirect interaction between parasitoids that develop inside different herbivore hosts sharing the food plant. However, this type of indirect plant-mediated interactions (IPMIs) among parasitoid larvae has received very little attention. In this study, we investigated sequential and simultaneous plant-mediated interactions among two host-parasitoid systems feeding on *Brassica oleracea* plants: *Mamestra brassicae* parasitized by *Microplitis mediator* and *Pieris rapae* parasitized by *Cotesia rubecula*. We measured the mortality, development time and weight of unparasitized herbivores and performance of parasitoids that had developed inside the two herbivore species when sharing the food plant either simultaneously or sequentially. Plant induction by parasitized or unparasitized hosts had no significant effect on the performance of the two herbivore host species. In contrast, the two parasitoid species had asymmetrical indirect plant-mediated effects on each other's performance. *Cotesia rubecula* dry weight was significantly increased by plants induced by *M. mediator*-parasitized hosts, while *M. mediator* development time was reduced by plant induced responses to conspecific but not to heterospecific parasitoids. Contrary to sequential feeding, parasitoids had no effect on each others performance when feeding simultaneously. These results reveal that indirect plant-mediated interactions among parasitoid larvae could involve any parasitoid species whose hosts share a food plant.

# Introduction

Plants have evolved several defensive strategies in order to mitigate the fitness cost of herbivore attack, such as the production of toxic chemical compounds induced by herbivory (Karban 2011). Induced plant defence strategies are often adapted to the attacker guild and/or species (Heidel and Baldwin 2004; Mewis et al. 2006; Kessler and Halitschke 2007). Upon damage, plants perceive and recognize herbivore-associated molecules in order to fine tune their response (Felton and Tumlinson 2008; Mithöfer and Boland 2008; Bonaventure 2012). As a result, plant induction by different herbivore species may result in plant phenotypic and quality differences. Over their lifetime, plants may interact with a range of species of herbivores (Mertens et al. 2021). The first induction of a plant early in the season will likely change its chemical phenotype and alter its quality, which can, in turn, indirectly affect subsequent herbivores feeding on the same plant (Kessler and Halitschke 2007; Ohgushi 2008). For example, early-season induction of *Brassica oleracea* plants by *Pieris rapae* caterpillars render plants more attractive to the specialist Lepidopteran herbivore *Plutella xylostella*, but not to the generalist *Mamestra brassicae* that colonize the plant later in the season (Poelman et al. 2008). These types of non-trophic interactions are termed 'indirect plant-mediated interactions' (IPMIs). They play an important role in how plants affect the structure of associated insect communities (Utsumi et al. 2010; Poelman and Dicke 2014; Stam et al. 2014).

However, plants also interact with insects from higher trophic levels, such as predators and parasitoids. Parasitoids are insects that develop inside (endoparasitoid) or outside (ectoparasitoid) a host which is either immobile or paralyzed (idiobiont parasitoid) or that is allowed to move and feed until parasitoid pupation (koinobiont parasitoid), whereas the adult stages are free-living (Godfray 1994). When they parasitize a host, koinobiont parasitoids inject several factors along with eggs, such as Polydnviruses (PDVs) and venom (Asgari and Rivers 2011; Strand and Burke 2019). These factors have a significant impact on the host development and physiology to optimize the environment for parasitoid larval development (Vinson and Iwantsch 1980; Beckage and Gelman 2004). As a consequence of this, koinobiont parasitoids modify the interaction between their host and the host-plant in different ways (Kaplan et al. 2016). They can mediate quantitative changes in herbivore damage, such as a reduction of the amount of plant tissue consumed by their host through a premature arrestment of the herbivorous host development (Harvey 1996; Beckage and Gelman 2004). Yet other parasitoids, e.g. gregarious parasitoid that lay many eggs in a single host, increase host biomass and plant damage by increasing feeding behaviour of their host and/or prolongating their development time (Ode 2006; Cuny and Poelman 2022). Moreover, parasitoids modify qualitative aspects of herbivory, such as the composition of the herbivore saliva (Poelman et al. 2011b; Tan et al. 2018, 2019). For example, *Pieris brassicae* caterpillars injected with *Cotesia glomerata* PDVs and venom exerted a reduced transcript level of genes related to the suppression of plant defence in their salivary glands (Cusumano et al. 2018; Zhu et al. 2018). In turn, plants induced by these caterpillars had a lower transcript level of plant-defence-related genes (Cusumano et al. 2018) and parasitoids affect plant nutritive quality including concentrations of chemical defences (Ode et al. 2016).

By indirectly affecting plant response to herbivory, parasitoids may, in turn, affect herbivores feeding on the same plant via IPMIs (Cusumano and Volkoff 2021; Poelman and Cusumano 2022). For example, plant-phenotypic changes induced by parasitized herbivores increase the performance of unparasitized herbivores and reduce the oviposition preference of adult herbivores compared to plants induced by unparasitized caterpillars (Poelman et al. 2011b; Cusumano et al. 2018, 2021). Furthermore, if two parasitized herbivores feed on the same plant, parasitoid larvae developing in different hosts can also affect each other through IPMIs. So far, such IPMI among parasitoid larvae have only been shown between two parasitoids species (*Cotesia rubecula* and *Cotesia glomerata*) sharing the same herbivorous host species (*Pieris rapae*) (Poelman et al. 2011a).

More research is needed to have a better understanding of IPMIs among parasitoid larvae in nature. Particularly, it is unknown whether this type of interaction can also happen between two parasitoid species that do not share the same host species (Poelman and Cusumano 2022). Additionally, IPMIs among parasitoids have only been tested sequentially, and virtually nothing is known about simultaneous feeding on the same plant.

In this study, we examined IPMIs between two host-parasitoid systems feeding on *Brassica oleracea* plants: *Mamestra brassicae* (Lepidoptera: Noctuidae) parasitized by *Microplitis mediator* (Hymenoptera: Braconidae) and *Pieris rapae* (Lepidoptera: Pieridae) parasitized by *Cotesia rubecula* (Hymenoptera:

Braconidae). We measured the effect of plant induction by parasitized and unparasitized caterpillars on the performance of unparasitized caterpillars as well as the two parasitoid species in their respective host species. We tested the hypothesis that parasitoids more prominently affect performance of other parasitoids when their hosts are feeding sequentially from the food plant rather than feeding simultaneously due to time lags in establishment of induced plant phenotypes. Our results provide important insights in how IPMIs could affect multitrophic interactions in natural and agricultural ecosystems.

## Materials And Methods

### Plants and insects

As host plants, we used wild cabbage *Brassica oleracea* which grows naturally along the coastline of England. Seeds were collected from the Kimmeridge population in Dorset, UK (Gols et al. 2008). This plant has been shown to respond differently to parasitized and unparasitized caterpillar hosts (Zhu et al. 2015). Plants were germinated and seedlings were transferred to 2-L pots containing peat soil (Lentse potgrond No. 4; Lentse Potgrond BV, Lent, The Netherlands). Pots were placed in a greenhouse, providing the plants with a 16:8 (light : dark) photoperiod with SON-T light (moles of quanta; 500  $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ ) (Philips, Eindhoven, The Netherlands) in addition to daylight, at 18–26°C and 40–70% relative humidity. When the plants were four weeks old, they were fertilized weekly with 100 mL of nutrient solution (Kristalon, Nutritech System, Moscow, Russia, concentration 3 g/L, [16N:6P:20K:3Mg]).

Two lepidopteran herbivore species were used in our experiments: *Pieris rapae* and *Mamestra brassicae*. *P. rapae* is a specialist feeding on Brassicaceae that is able to deal with high levels of glucosinolates (i.e. plant secondary metabolites) (Smallegange et al. 2007), while *M. brassicae* is considered a generalist and is less adapted to this type of chemical defense (Gols et al. 2008).

We used two solitary endoparasitoids from the Braconidae family that do not share the same host and are both considered as specialists. *Cotesia rubecula* parasitizes *P. rapae* (Brodeur et al. 1998), while *Microplitis mediator* parasitizes *M. brassicae* (Malcicka and Harvey 2014). All insects were routinely cultured on *Brassica oleracea* Cyrus under greenhouse conditions (18–26°C and 40–70% relative humidity).

### Experimental approach

To unravel whether parasitoids that develop in one herbivore host species may affect parasitoids developing in a different one when feeding on the same food plant, we conducted two experiments (Fig. 1). In the first experiment we focused on how each parasitoid species developing in its respective host caterpillar affects development of subsequently feeding caterpillars of both host species. In the second experiment, we tested whether parasitoids developing in their respective host species affect conspecific or heterospecific parasitoids developing in a second herbivore feeding either simultaneously or sequentially from the same food plant. Together the results of these experiments reveal whether

parasitoids affect each other via performance effects on each other's host or that these effects are more intricate without affecting host herbivore performance traits.

## First experiment: plant-mediated effects on unparasitized herbivores

Six-week-old *B. oleracea* plants were individually covered with a net and infested with a first round of herbivory according to one of the following treatments (sixteen plants per treatment): 1) no herbivory, 2) six unparasitized *P. rapae*, 3) six *P. rapae* parasitized by *C. rubecula*, 4) six unparasitized *M. brassicae*, or 5) six *M. brassicae* parasitized by *M. mediator*. Neonate caterpillars of each species were individually parasitized (Poelman et al. 2014) by their corresponding parasitoid one day prior to plant infestation. After nine days when the parasitoid larvae were full grown and nearly all of them had egressed from their caterpillars for pupation, we removed all herbivores from all the plant treatments. Two days later, we infested half of the plants from each treatment (eight plants) with ten unparasitized *P. rapae*, and the other eight plants with ten unparasitized *M. brassicae*. This second round of herbivory was used to measure host performance. *P. rapae* were allowed to develop on the plant until pupation, while *M. brassicae*, which pupate in the soil, were transferred into boxes with one cm of soil when they reached the wandering stage in search of a pupation site. Performance was assessed by i) fresh weight of the pupae, ii) adult emergence time from introduction of the caterpillars onto the plant, and iii) mortality rate, i.e. number of caterpillars not developing into adults relative to the number that were initially introduced. Pupae of both herbivores were stored in plastic tubes at 22°C to measure development time until adult emergence.

## Second experiment: plant-mediated effects on parasitoids

Six-week-old *B. oleracea* plants were infested with the same five main treatments as mentioned above, with thirty plants per treatment that were each covered by a net to prevent herbivores from moving to neighboring plants. After nine days when nearly all parasitoids had egressed from their caterpillars, we removed all herbivores from all the plant treatments. Two days after removing all the insects from the plants, half of the plants from the five main treatments received six *P. rapae* parasitized by *C. rubecula*, while the other half received six *M. brassicae* parasitized by *M. mediator* (fifteen plants per treatment). Parasitoid cocoons were collected and individually placed in plastic tubes and checked for emergence five times per day. To quantify parasitoid performance, we measured i) difference in parasitoid development time (in hours, starting from the first adult parasitoid emergence), and ii) adult dry weight. The sex of the adult parasitoids was determined under a stereomicroscope. Before measuring parasitoid dry mass on a microbalance, the parasitoids were dried for 2 days in an oven at 80 °C.

## Second experiment: effects of herbivore density and timing on plant-mediated interactions between parasitoids

In addition to the five treatments described above, fifteen other plants were infested with only three unparasitized *P. rapae* during the first round of herbivory (instead of 6). After pupation, the caterpillars

were removed and the plants received six *M. brassicae* parasitized by *M. mediator*. This treatment was used to compare how the amount of herbivory, i.e. three or six *P. rapae* feeding during the first round of herbivory, affects plant-mediated effects on parasitoids. Thirty additional undamaged plants were left without insects during the first round of herbivory and received simultaneously three parasitized *P. rapae* and three parasitized *M. brassicae*. This treatment was used to compare how time interval, i.e. simultaneous feeding or eleven days between feeding by parasitized caterpillars, affects plant-mediated interactions among parasitoids that develop in different host herbivores on the same food plant. The performance of parasitoids was measured as described above both for effect of herbivory density and timing of herbivory.

## Statistical analyses

In all our models, we used plant-induction treatment as a fixed factor and plant individual as a random factor. We used linear mixed models to analyze the development time of herbivores and parasitoids, except for unparasitized *M. brassicae* in the first experiment. Because of the non-normal distribution of the residuals of these data, we used a generalized linear mixed model with a Poisson distribution. The mortality of unparasitized caterpillars and parasitoids was analyzed using generalized linear mixed models with a binomial distribution, while we analyzed their weight with linear mixed models. We analyzed the dry weight of males and females jointly for *Cotesia rubecula* because of a low female ratio. All statistical analyses were performed with R (version 4.0.4, R Core Team 2021), using the lme4 packages for mixed models.

## Results

### First experiment: plant-mediated effects on unparasitized herbivores

Feeding by a first generation of parasitized or unparasitized *P. rapae* and *M. brassicae* caterpillars had no plant-mediated effects on the development time ( $\chi^2_{(4)} = 7.8$ ,  $P = 0.097$ ), mortality ( $\chi^2_{(4)} = 2.12$ ,  $P = 0.71$ ) and pupal weight ( $\chi^2_{(4)} = 4.94$ ,  $P = 0.29$ ) of unparasitized *P. rapae* that were subsequently feeding from the induced plants. Similar results were found for the development time ( $\chi^2_{(4)} = 0.06$ ,  $P = 0.99$ ), mortality ( $\chi^2_{(4)} = 1.52$ ,  $P = 0.82$ ) and pupal weight ( $\chi^2_{(4)} = 1.04$ ,  $P = 0.90$ ) of unparasitized *M. brassicae* (Fig. 2).

### Second experiment: plant-mediated effects on parasitoids

Mortality ( $\chi^2_{(4)} = 4.72$ ,  $P = 0.32$ ) and development time ( $\chi^2_{(4)} = 3.82$ ,  $P = 0.43$ ) of *C. rubecula* was not affected by induction treatment. However, the dry weight of adult *C. rubecula* was significantly higher when their hosts were feeding on a plant that had been induced by *M. brassicae* larvae parasitized by *Microplitis mediator* compared to control plants ( $\chi^2_{(4)} = 14.22$ ,  $P = 0.007$ ) (Fig. 3). Dry weights of *C.*

*rubecula* on the other three induction treatments were intermediate, but did not differ from those on the no-herbivory and *M. brassicae*-*M. mediator*-induction treatment (Fig. 3).

Plant induction treatments had no significant effect on the mortality ( $\chi^2_{(5)} = 6.89$ ,  $P = 0.23$ ) and dry weight of *M. mediator* adult parasitoids, both for females ( $\chi^2_{(5)} = 5.65$ ,  $P = 0.34$ ) and males ( $\chi^2_{(5)} = 4.68$ ,  $P = 0.46$ ). Development time of *M. mediator* was significantly shorter when their hosts were feeding on control plants and plants induced by *M. brassicae* caterpillars parasitized by conspecific parasitoids compared to plants induced by unparasitized *M. brassicae* ( $\chi^2_{(5)} = 20.94$ ,  $P < 0.001$ ) (Fig. 4). The heterospecific parasitoid *C. rubecula* and its host *P. rapae* did not significantly affect performance of *M. mediator* developing in *M. brassicae*.

## Second experiment: timing but not density affects plant mediated interactions between parasitoids

The lower density of unparasitized *P. rapae* caterpillars (three) was not statistically different from the higher density (six) and had no significant effect on the development time, mortality and adult female and male dry weight of *M. mediator* parasitoids developing in *M. brassicae* (Fig. 4).

Contrary to sequential feeding, parasitized *P. rapae* and *M. brassicae* caterpillars feeding simultaneously on the same food plant that was not previously induced did not affect each other's performance (Fig. 5). We found no significant effect of simultaneous feeding on the parasitoids mortality (*M. mediator*:  $\chi^2_{(1)} = 0.34$ ,  $P = 0.56$ ; *C. rubecula*:  $\chi^2_{(1)} = 0.62$ ,  $P = 0.43$ ), development time (*M. mediator*:  $\chi^2_{(1)} = 0.98$ ,  $P = 0.32$ ; *C. rubecula*:  $\chi^2_{(1)} = 0.06$ ,  $P = 0.8$ ) and adult dry weight (*M. mediator* males:  $\chi^2_{(1)} = 1.51$ ,  $P = 0.22$ ; *M. mediator* females:  $\chi^2_{(1)} = 0.85$ ,  $P = 0.36$  *C. rubecula*:  $\chi^2_{(1)} = 0.25$ ,  $P = 0.61$ ) compared to feeding alone.

## Discussion

Previous damage by parasitized and unparasitized caterpillars on *B. oleracea* plants did not affect performance of unparasitized *P. rapae* and *M. brassicae* subsequently feeding on the same plant. Contrary to their host, when the subsequent herbivores feeding on the induced plants were parasitized, we found that induction with *M. brassicae* parasitized by *M. mediator* affected both parasitoid species positively. Dry weight of *C. rubecula* was significantly increased when feeding on plants previously induced by *M. mediator*-parasitized herbivores, compared to undamaged plants. However, no plant-mediated effects were observed on the performance of parasitoids when parasitized caterpillars fed simultaneously on the same food plant. On the other hand, *M. mediator* parasitoids developed significantly faster when their hosts were feeding on plants induced by conspecific parasitized hosts, with no effect of plant induction by *C. rubecula*.

## Interactions are asymmetrical and facilitating

We observed an asymmetrical, facilitating IPMI between two parasitoid species with different hosts. Plant induction by *M. mediator*-parasitized herbivores positively affected the dry weight of *C. rubecula* parasitoids. On the contrary, *M. mediator* parasitoids were not affected by plants induced by *C. rubecula*-parasitized herbivores. In a similar study, an asymmetrical sequential IPMI was found between *Cotesia glomerata* and *C. rubecula* parasitoids developing in *P. rapae* larvae on *B. oleracea* plants (Poelman et al. 2011a). Yet, in this case, *C. rubecula* had an antagonistic effect on the survival of *C. glomerata* and no effects were found on performance of *C. rubecula*. The asymmetrical antagonistic IPMIs between two parasitoid species with overlapping host ranges could be adaptive in order to limit competition for hosts when the parasitoid emerge (Poelman et al. 2011a).

We also found a facilitating IPMI between conspecific parasitoids. *Microplitis mediator* significantly reduced the development time of subsequent conspecific parasitoids developing on the same plant. Such facilitation could be the result of an adaptive extended phenotype of the parasitoids that alter plant response via their host (Cusumano et al. 2018; Zhu et al. 2018) in order to increase performance of their host and as a result of this their own fitness (Tan et al. 2018; Cusumano et al. 2021). Alternatively, parasitoids are under a strong selective pressure to modify their host physiology, which optimizes parasitoid larval development. Therefore, the observed IPMIs among parasitoid larvae could only be by-products of physiological changes upon parasitism, without evolutionary pressure, resulting in unpredictable outcomes of IPMIs among parasitized herbivores (Cuny et al. 2022).

## Interactions are especially sequential, and only affect parasitoids

Our results revealed three important characteristics of IPMIs by parasitoid larvae from two different systems: i) they were only apparent under sequential herbivory, ii) they had no effect on unparasitized hosts from the two systems and iii) they were not affected by the quantity of herbivory. Parasitized caterpillars simultaneously feeding on the same plant did not result in IPMIs between parasitoids. This was particularly clear for the dry weight of *C. rubecula* that was significantly increased by the previous feeding of *M. mediator*-parasitized caterpillars, but not when feeding simultaneously. In response to insect feeding, *B. oleracea* plants slowly increase their levels of glucosinolates during up to two weeks (Gols et al. 2018). Therefore, simultaneous feeding of caterpillars on the same plant may be too short to observe an effect on their performance. No other study tested the effects of simultaneous feeding of parasitized herbivores.

Parasitized caterpillars from the two systems had no apparent effect via IPMIs on subsequent unparasitized caterpillars. In general, parasitoids are less adapted to changes in plant quality than their host (Turlings and Benrey 1998; Ode 2006; Gols et al. 2008), which could explain our results. In a similar study, Poelman et al. (2011a) also found no effect of previous induction by unparasitized and *C. rubecula*-parasitized *P. rapae* on the performance of subsequent unparasitized *P. rapae*. However, *P. rapae* developmental time was significantly increased when feeding on plants induced by *C. glomerata*-parasitized larvae, compared to undamaged plants. In another study (Cusumano et al. 2021), plants



induced by parasitized caterpillars increased the performance of unparasitized ones, but the experimental design differs from ours as unparasitized caterpillars were fed with cut leaves induced by mechanical damage and saliva and the relative growth rate of caterpillars was measured after 48 hours.

Finally, 50% reduction of feeding damage by *P. rapae*, did not affect the performance of subsequent *M. mediator* parasitoids developing in *M. brassicae*. This result suggests that the effects of IPMIs among parasitoids are caused by qualitative changes in the herbivorous host and food plant, and not by quantitative effects on herbivore growth or by variation in amount of leaf damage by herbivores. However, it has to be noted that we only tested two caterpillar densities and that negative effects caused by quantitative changes could eventually arise with more damage.

## Implications

Parasitoids are ubiquitous in many natural and agricultural ecosystems in which they play an important role in structuring trophic interactions. In this study, we contribute to the awareness that different parasitoid species are involved in complex indirect non-trophic interactions mediated by plants. We fine-tuned the theory about this phenomenon by showing that 1) IPMIs between parasitoids may lead to facilitation in addition to the known antagonistic outcome (Poelman et al. 2011a); 2) simultaneous feeding of parasitized caterpillars on the same plant may be too short for plant induction to have an apparent effect on their performance, as it is the case in sequential feeding; 3) contrary to parasitoids, their herbivorous hosts were not affected by IPMIs; and 4) qualitative rather than quantitative changes in herbivory induced by parasitoids seem to be responsible for the effects observed in IPMIs among parasitoids.

Our work identifies that even parasitoids that were thought to never interact because of their different host ranges, can be involved in IPMIs as long as their respective herbivorous hosts share a common food plant. As a result, IPMIs among parasitoid larvae may be even more widespread than previously thought and should be recognized as an important indirect interaction type in food webs.

## Declarations

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### Conflict of interest

The authors declare no conflicts of interest.

### Availability of data

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

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## Authors' contribution

EP conceived and designed the experiments. RP, RG and EP performed the experiments. MC analyzed the data and wrote the manuscript. All authors revised the manuscript.

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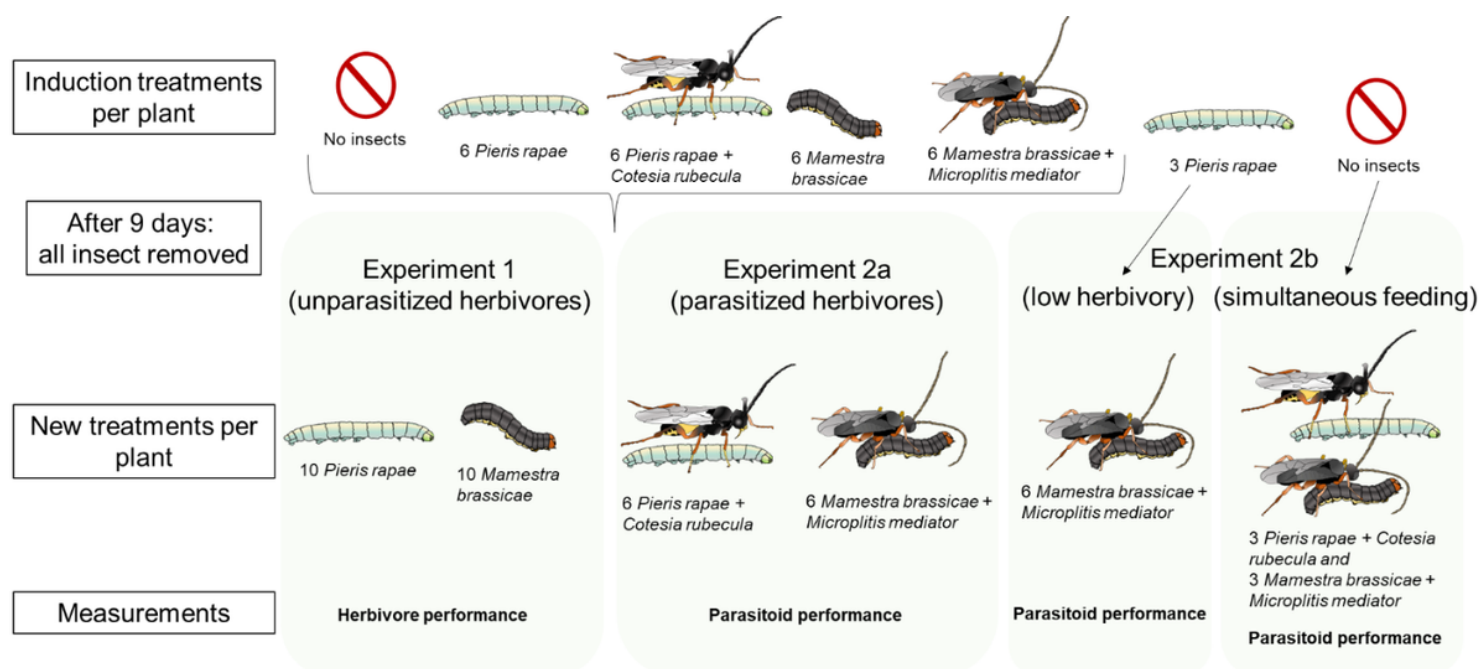
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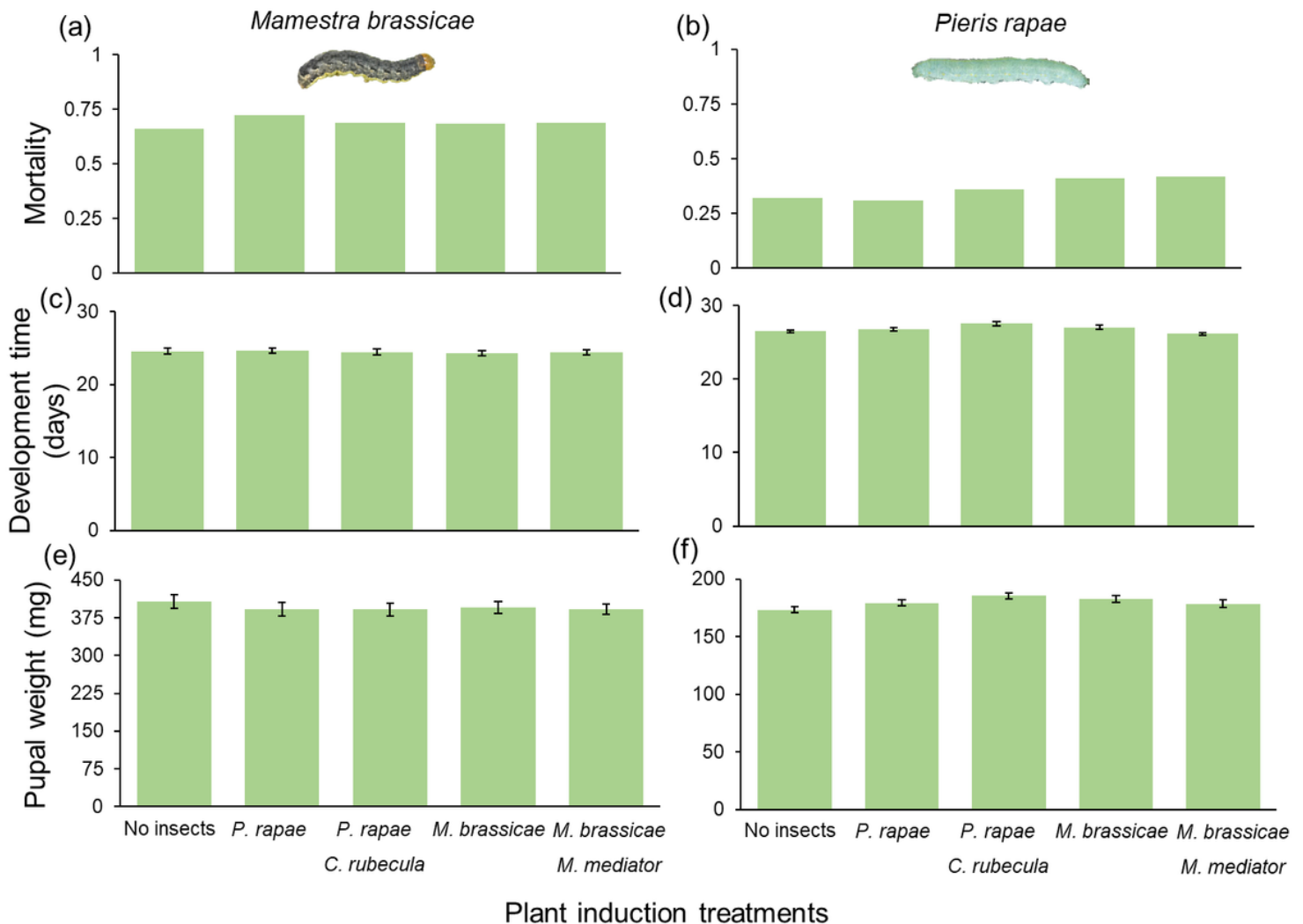
## Figures



**Figure 1**

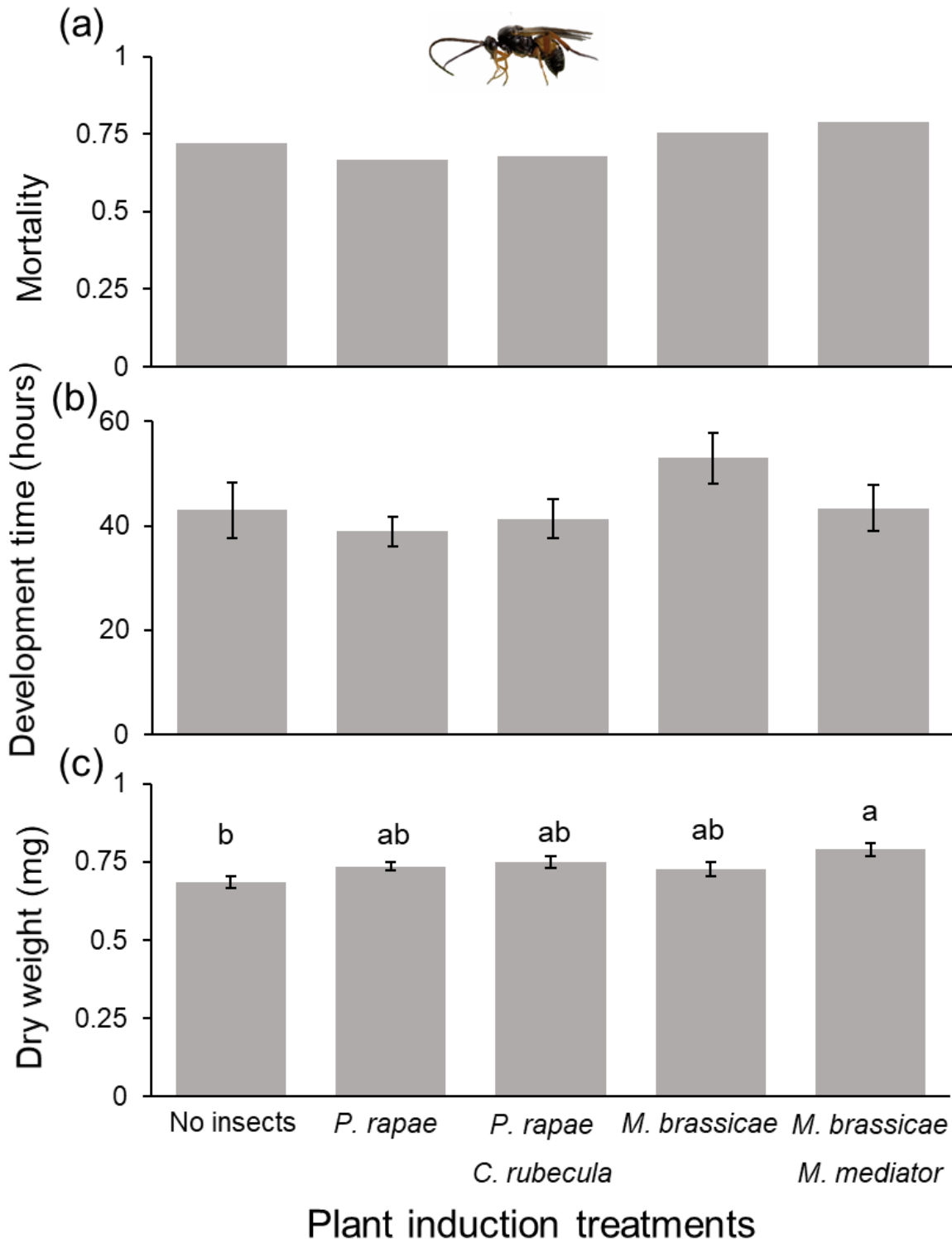
Experimental design to investigate plant-mediated interactions among parasitoid larvae of *Cotesia rubecula* and *Microplitis mediator* that develop in two different herbivore species, *Pieris rapae* and *Mamestra brassicae*, respectively. *Brassica oleracea* plants were left unchallenged (no insects) or were

induced by unparasitized or parasitized herbivores. In experiment 1, the induced plants were used to identify how caterpillars and parasitoids developing in a herbivore affect performance of new unparasitized caterpillars that feed sequentially on the plant. In experiment 2, the induced plants were offered to parasitized herbivores to identify how parasitoids developing in different herbivores affect each other (2a). We included two additional treatments to test if parasitoids affect each other's performance when their hosts feed simultaneously from the same food plant and manipulated density of the first batch of parasitized caterpillars to study how interactions are affected by herbivore density (2b).



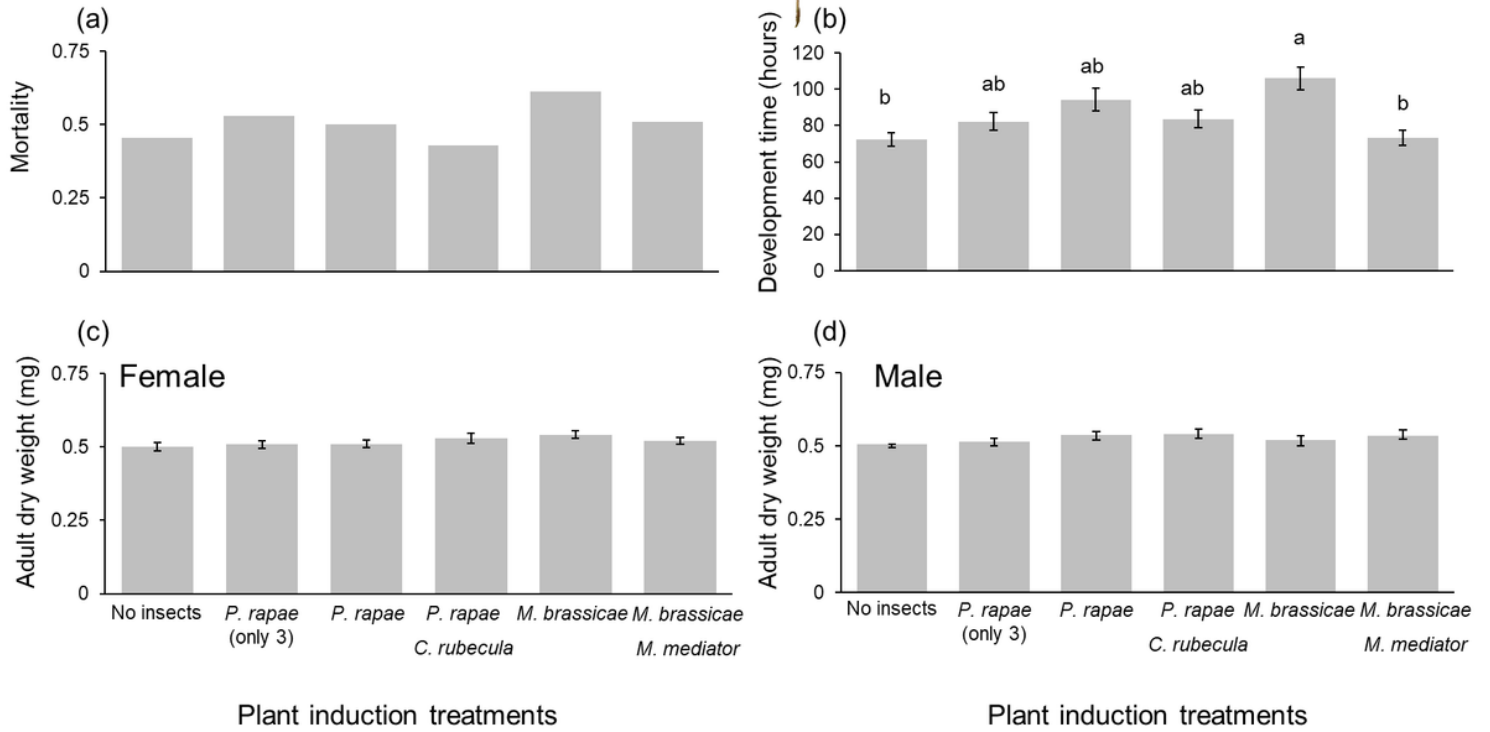
**Figure 2**

Performance parameters of *Mamestra brassicae*(a,c,e) and *Pieris rapae* (b,d,f) developing on *Brassica oleracea* plants that received different induction treatments. Bars are means ( $\pm$ SEM).



**Figure 3**

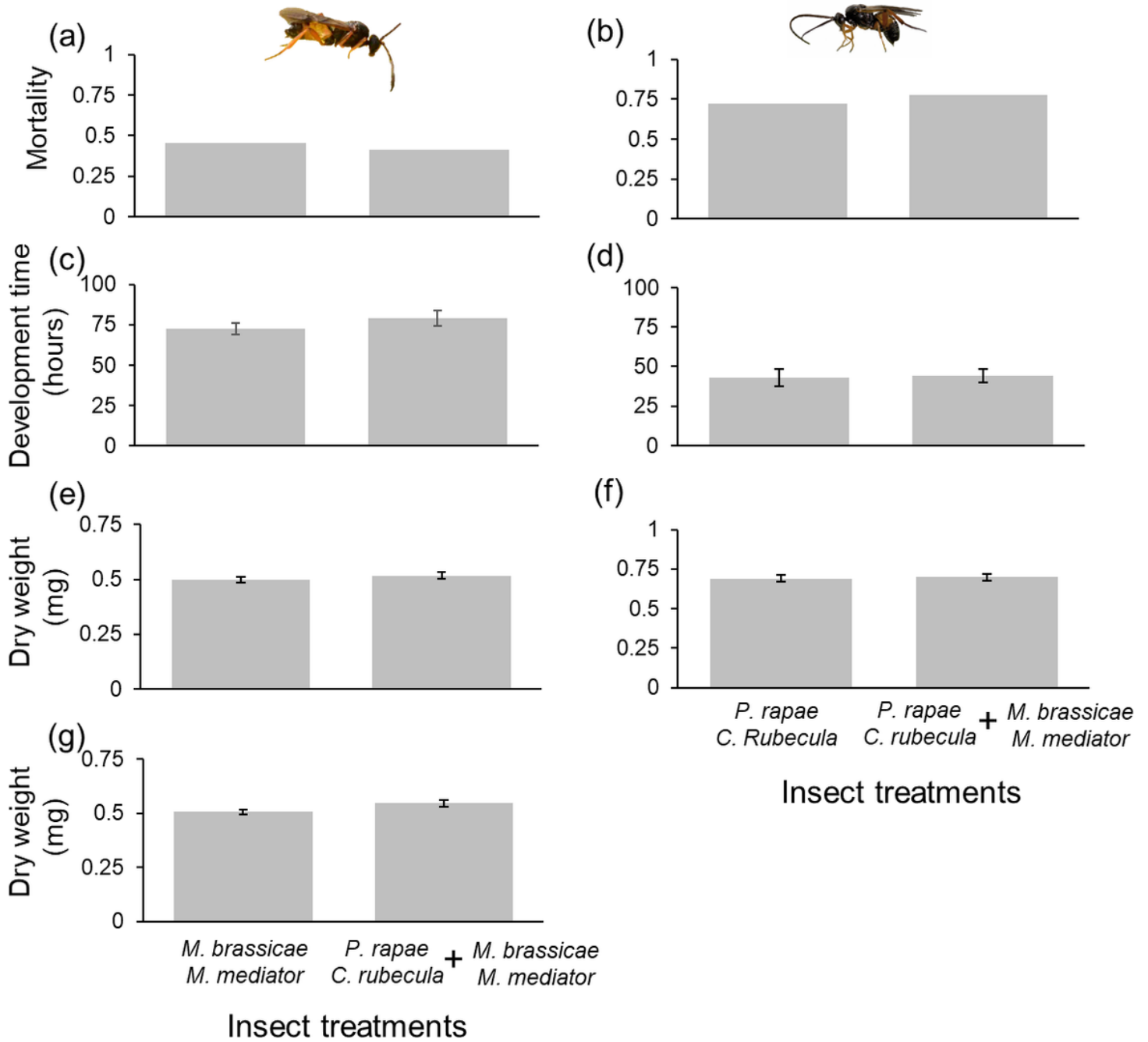
Performance parameters of *Cotesia rubecula* parasitoids whose host fed on plants previously induced by different treatments of parasitized and unparasitized caterpillars. (a) mortality ratio of *C. rubecula*, (b) development time measured in hours from oviposition until adult emergence and (c) *C. rubecula* adult dry weight. Bars are means ( $\pm$ SEM). Different letters indicate significant differences.



**Figure 4**

Performance parameters of *Microplitis mediator* parasitoids whose host fed on plants previously induced by different treatments of parasitized and unparasitized caterpillars, including a treatment with only three *P. rapae* (instead of six). (a) mortality ratio of *M. mediator*, (b) development time measured in hours from oviposition until adult emergence and (c) female *M. mediator* adult dry weight and (d) male *M. mediator* adult dry weight. Bars are means ( $\pm$ SEM). Different letters indicate significant differences.





**Figure 5**

Performance parameters of *Microplitis mediator* (left) and *Cotesia rubecula* (right) parasitoids whose hosts fed on untreated plants, either alone or simultaneously with parasitized caterpillars from the other system. (a) mortality ratio of *M. mediator*, (b) mortality ratio of *C. rubecula*, (c) development time measured in hours from the first *M. mediator* adult emergence, (d) development time measured in hours from the first *C. rubecula* adult emergence, (e) *M. mediator* male adult dry weight, (f) *C. rubecula* adult dry weight (both males and females) and (g) *M. mediator* female adult dry weight. Bars are means ( $\pm$ SEM).