Plant-mediated effects of butterfly egg deposition on subsequent caterpillar and pupal development, across different species of wild Brassicaceae

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Abstract. 1. Herbivory can change plant quality, which may have consequences for interactions between the inducing herbivore and other insect community members.

2. Studies investigating the effects of plant quality on herbivore performance often have neglected the egg stage, and instead introduced larvae onto the plant. Recently, we reported that herbivore oviposition by *Pieris brassicae* (Linnaeus) (Large Cabbage White Butterfly) reduced the plant quality of *Brassica nigra* L. (black mustard) for subsequent herbivores.

3. It remains unclear how persistent and common these plant-mediated effects of oviposition are. Here, five species of wild Brassicaceae were used (*B. nigra L., Brassica oleracea L., Sinapis arvensis L., Moricandia arvensis L.,* and *Moricandia moricandioides Boiss*). The response to oviposition by the specialist *P. brassicae* was determined by following the natural sequence of events: oviposition, egg, larval, and pupal development. All tested plant species are known to interact with *P. brassicae* in nature. Caterpillar, pupal mass, and development time on plants exposed to butterfly eggs were assessed compared with egg-free plants.

4. It was shown that the plant-mediated effects of oviposition are not specific for *B. nigra* but occur in most of the tested plant species except for *M. arvensis*. However, the strength of the plant-mediated effect on caterpillar growth depended on plant species. Thus, across different members of the Brassicaceae family, oviposition can influence plant quality and has negative consequences on *P. brassicae* growth. Further studies are needed to assess to what extent this trait might be phylogenetically conserved.

Key words. Brassicaceae, egg deposition, insect performance, specialist herbivore, variation.

Introduction

Plant species and populations display variation in resistance traits, which mediate interactions with their insect communities (Lankau & Strauss, 2007; Gols *et al.*, 2009). These resistance traits, physical or/and chemical, are classified according to the timing of deployment into (i) traits that are *constitutively* produced and (ii) traits that are *induced* upon herbivore attack or a combination of the two (Gatehouse, 2002; Wu & Baldwin, 2010). Induced plant responses are considered to reduce allocation costs as they are only employed when the plant is under attack (Poelman & Dicke, 2014).

For many insect–plant systems, it has been shown that induced plant responses change plant quality, impairing growth and survival of herbivores and hampering colonisation by subsequently arriving herbivores (Karban & Baldwin, 1997; Gols & Harvey, 2008; Howe & Jander, 2008). The term host-plant quality is used to describe the positive or negative effects of plant compounds (e.g. nitrogen, carbon levels, and defensive compounds) on herbivore performance (Awmack & Leather, 2002).

Induced plant responses can have consequences for successive interactions with herbivores and other species in the plant-associated community (van Zandt & Agrawal, 2004;

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Viswanathan *et al.*, 2005; Kaplan & Denno, 2007; Poelman *et al.*, 2011; Stam *et al.,* 2014). These plant-mediated interactions can influence insects at different trophic levels associated with above or belowground tissues (van der Putten *et al.*, 2001; Bezemer & van Dam, 2005; Poelman *et al.*, 2011; Erb *et al.*, 2011). In addition, herbivores of different feeding guilds (Soler *et al.*, 2012; Kaplan & Denno, 2007) and often herbivores' sequence of arrival can also induce plant changes (Poelman *et al.*, 2008a,2008b; Erb *et al.*, 2011). There is ample literature reporting that induced plant responses, both morphological and chemical, can be herbivore-species specific (Karban & Baldwin, 1997; Agrawal, 2000; van Zandt & Agrawal, 2004; Viswanathan *et al.*, 2005; Uesugi *et al.*, 2013) and herbivores may respond differentially to these induced changes (Karban & Baldwin, 1997).

Plants respond to egg deposition by herbivorous insects, which in most species precede larval feeding, by increasing defences that can impair egg development or even kill the eggs directly or indirectly by recruiting egg parasitoids (Hilker & Fatouros, 2015). These egg-killing defence mechanisms of plants [e.g. hypersensitive response (HR), necrotic lesions surrounding the eggs] have been described for more than 20 insect species in more than 20 different plant species (Hilker & Fatouros, 2015). However, plant-mediated effects of egg deposition on subsequent herbivores during different developmental stages (i.e. from larvae to adults) and their interactions with other trophic levels have only recently been discovered in *Pinus sylvestris* L., *Arabidopsis thaliana* L., and *Brassica nigra* L. (Bruessow *et al.*, 2010; Beyaert *et al.*, 2011; Geiselhardt *et al.*, 2013; Pashalidou *et al.*, 2013, 2015; Hilfiker *et al.*, 2014).

Caterpillars of Cabbage White Butterflies, *Pieris spp.,* are voracious herbivores. The later stages of *P. brassicae* prefer to feed on the flowers of their brassicaceous host plants with potential negative consequences for plant fitness (Smallegange *et al.*, 2007). Plants that respond to herbivores when these are still in the egg stage may, therefore, receive less herbivore damage and produce more flowers (Pashalidou *et al.*, 2013) or produce seeds earlier (Lucas-Barbosa *et al.*, 2012), i.e. they display a reproductive escape. However, it remains unknown whether plant-mediated effects of oviposition on subsequent herbivory are an intrinsic trait across different brassicaceous species.

The aim of this study was to explore whether herbivore egg deposition induces changes in plant quality that affect subsequent life stages of the herbivore (larvae and pupae) in different brassicaceous plant species. We selected the following five wild species: *Brassica oleracea* L., *B. nigra* L., *Sinapis arvensis* L., *Moricandia arvensis* L. and *M. moricandioides* Boiss. *Brassica oleracea* is a perennial plant with a glabrous waxy leaf surface and the plant quality for insect herbivores varies among populations of this plant species (Gols *et al.*, 2008). *Brassica nigra* and *S. arvensis* are annuals with non-waxy leaves that often carry trichomes. Both *Moricandia* species are annual plants with waxy leaves. All plant species used in this study are known to interact with *P. brassicae* in nature (Courtney & Chew, 1987). *Pieris brassicae* is a gregarious herbivore, native in Europe, and usually lays clutches of 40 or more eggs on the abaxial side of the leaves (Feltwell, 1982).

We compared herbivore development on plants infested with *P. brassicae* eggs that were allowed to develop into larvae, with plants, where neonate larvae of *P. brassicae* were introduced. As proxies for herbivore fitness, we measured larval and pupal biomass and egg-to-pupal development time.

Materials and methods

Plants and insects

We used two populations of *Brassica oleracea*, *Sinapis arvensis* and *Brassica nigra* respectively, and single populations of *Moricandia moricandioides* and *M. arvensis*.

Brassica nigra seeds were collected from naturally growing populations at two different locations about 8 km apart, one near Heteren (coordinates: 51.951, 5.7083) and one near Wageningen (51.9666, 5.6666), the Netherlands.

Seeds of *S. arvensis* were collected from two naturally growing wild populations, one on the island of Vlieland (53.3, 5.0666) in the northern part of the Netherlands and one from Buren (53.4472, 5.7988), located in the riverine area of the Netherlands.

Seeds of two wild populations of *B. oleracea* were collected along the South coast of England, to the West and North of Swanage, Dorset at locations that are known as Kimmeridge (50.617, −2.118) and Winspit (50.5848, −2.0342).

Moricandia moricandioides and *M. arvensis* grow in arid habitats. Seeds were collected in Albacete province, South-East Spain.

Two cohorts of 15 plants of the above-described species and populations were grown in successive weeks starting at the end of February until the last week of April 2012. Seeds were germinated and the seedlings were transferred to pots filled with potting soil. Plants were grown in a greenhouse ($18 \pm 4\,°C$, 60–80% RH, LD 16:8) and were watered daily. *Brassica oleracea* plants, which grow more slowly than the other four plant species, were 5 weeks old, whereas the other plant species were 4 weeks old at the beginning of the experiments.

The butterflies were from our laboratory colony initially collected from Brussels sprouts plants (*Brassica oleracea* var. *gemmifera*). *Pieris brassicae* was reared in a climatised room ($22 \pm 1\,°C$, 50–70% RH, LD 16:8) on Brussels sprouts plants, *B. oleracea* var. *gemmifera* cv. Cyrus.

Plant treatments

Butterflies of *P. brassicae* were allowed to lay eggs on half of the experimental plants. Plants from each tested population or species were individually placed in a rearing cage with approximately 100 butterflies. Oviposition was carefully observed and the number of eggs laid on the plants were counted. When females had laid approximately 20 eggs, the plant [eggs(+): plant exposed to oviposition] was removed from the cage. Additional eggs, if any, were removed gently with a fine brush within 20 min after oviposition. A previous study has shown that the eggs and not airborne signals, scales or any other source from

the butterflies induced the plants and affected caterpillar development, as larval growth was not affected when all eggs had been removed immediately after oviposition (Pashalidou *et al.*, 2013). Plants that had no contact with butterflies or any other insect were used as a control [eggs(−) plants: plant not exposed to oviposition]. All plants were kept in a greenhouse ($18 \pm 4\,°C$, 60–80% RH, LD 16 : 8). In total, 30 plants were used per population or species [15 eggs(+)- and 15 eggs(−) plants], apart from *M. arvensis* where 16 plants were used owing to a low germination rate [8 eggs(+)- and 8 eggs(−) plants]. Plants were visually inspected for a hypersensitive response (HR)-like necrosis to eggs 3 days after oviposition and the percentage of plants expressing HR was calculated.

Plants were treated as previously described in Pashalidou *et al.* (2013). Briefly, when *P. brassicae* caterpillars emerged from eggs on an eggs(+) plant, 10 neonates were transferred with a fine brush to the adaxial side of the same leaf. Another 10 caterpillars were transferred to the adaxial leaf-side of an eggs(−) plant. Each caterpillar from each plant was weighed 7 days after hatching on a microbalance (accuracy = 1 μg) (Sartorius AG, Göttingen, Germany). Because *P. brassicae* caterpillars can consume the entire plant in a few days depending on the size of the plant and caterpillar density, we transferred only three caterpillars back to the same plants after the first biomass measurement (7 days after hatching). Caterpillars were allowed to move and feed freely on the plants. As caterpillars tend to disperse in the final larval stage to find a site for pupation, plants were covered with fine nets 5 days before pupation. Larvae were inspected regularly and when they pupated, the date of pupation was recorded and pupae were weighed on an analytical balance (accuracy 0.1 mg, Mettler Toledo) 1 day later to allow the pupal cuticle to sclerotise.

As fitness proxies we compared (i) biomass of *P. brassicae* caterpillars 7 days after hatching, (ii) pupal biomass, and (iii) the development time from egg to pupa between the different plant populations and across species both on eggs(+) and eggs(−) plants.

Statistical analysis

The performance data, larval and pupal mass, and developmental time, respectively, were statistically analysed using a linear mixed model (LMM):

$$Y_{ijk} = \mu + \alpha_i + \beta_j + \alpha\beta_{ij} + d_{ij} + e_{ijk}$$

where Y_{ijk} is the observed value (Y_{ijk}: caterpillar mass, pupal mass, or development time), μ is the general mean, α_i the fixed effect of the plant species, level i (i = *B. nigra, S. arvensis, B. oleracea, M. arvensis*, and *M. moricandioides*), β_j the fixed effect of plant treatment, [j = eggs(+), eggs(−)], and $\alpha\beta_{ij}$ the interaction term. The two random terms in the model correspond to variation among populations nested within plant species d_{ij} (σ_d^2) and the variation among caterpillars developing on a single plant (= biological replicate) e_{ijk} (σ_e^2). An additional LMM analysis was performed on the insect performance data obtained for each of the five tested plant species to test for the effect of egg induction within each plant species. Plant treatment was entered as a fixed model factor, whereas population (*B. nigra, B. oleracea*, and *S. arvensis*) and plant individual were entered as random factors. Model fitting was done by employing restricted maximum likelihood (REML) and statistical tests for fixed effects were based on approximated *F*-tests. Normality, independence, and homogeneity of variance were checked by inspection of the residuals after fitting the model. The data on *B. nigra* were subjected to an additional analysis to determine the effect of the HR-like response. We used a similar statistical model as described above in which we included an additional fixed term for a HR-like response (yes/no) and removed the plant species term.

All analyses were conducted using the R software version 2.13.1 and lme4 package (R Development Core Team, 2008).

Results

Egg-induced hypersensitive response (HR)

Pieris brassicae eggs induced HR-like necrosis in both plant species with non-waxy pubescent leaf surfaces (*B. nigra* and *S. arvensis*), whereas it was weak or not observed in plant species with glabrous waxy surfaces (*B. oleracea* and *Moricandia* spp.). HR expression was the strongest in *B. nigra* where 47–73% of the plants expressed HR (Table 1).

Effects on larval biomass

Egg induction ($F_{1,4} = 63.4$, $P < 0.001$), plant species ($F_{1,4} = 13.8$, $P < 0.001$), and their interaction ($F_{1,4} = 9.05$, $P < 0.001$) had a significant effect on larval biomass. Egg induction reduced food quality in all plant species but not to the same extent (Fig. 1a, Tables S1 and S2). The effect of egg induction was highly significant in *M. moricandioides, B. nigra*, and, *B. oleracea,* almost significant in *S. arvensis* ($F_{1,4} = 3.54$, $P = 0.06$, Table S2) and not significant in *M. arvensis* ($F_{1,4} = 0.31$, $P = 0.58$, Table S2). Moreover, plant species itself also influenced larval mass; caterpillar performance was higher in *B. nigra* plants compared with *B. oleracea* and *M. arvensis,* and *S. arvensis* (Fig. 1a, Table S2). In *B. nigra,* egg-induced HR had no subsequent effect on larval mass ($F_{1,1} = 0.19$, $P = 0.65$).

Table 1. Percentage of plants expressing hypersensitive response (HR)-like necrosis induced by *Pieris brassicae* oviposition in five brassicaceous plant species.

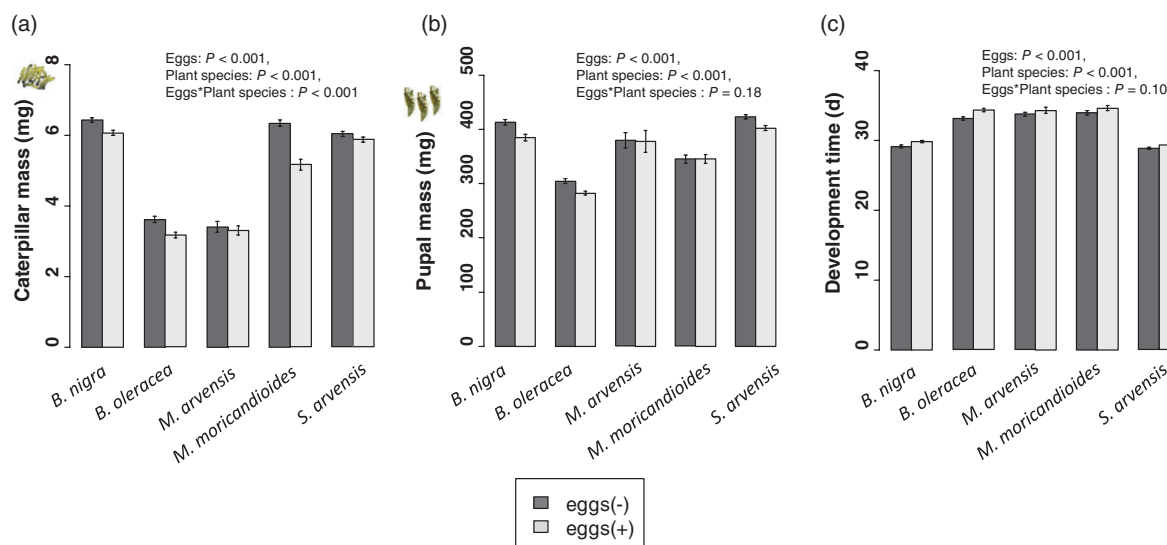| Plant species	Population	HR (%)	N tested
Sinapis arvensis	Vlieland	20	15
	Buren	27	15
Brassica nigra	Heteren	73	15
	Wageningen	47	15
Brassica oleracea	Kimmberidge	7	15
	Winspit	0	15
Moricandia arvensis	–	0	8
Moricandia moricandioides	–	0	15

Fig. 1. Plant-mediated effects of *Pieris brassicae* oviposition on the performance of larvae and pupae. Bars (mean ± SE) indicate the body mass (mg) of *P. brassicae* (a) 7-day-old caterpillars, (b) pupae, and (c) egg-to-pupa development time (days) on different plant species (*B. nigra, B. oleracea, S. arvensis, M. arvensis, M. moricandioides*). *Pieris brassicae* developed on plants previously infested with eggs [eggs(+): light grey bars] or on egg-free plants [eggs(−): dark grey bars]; the statistical results refer to general linear mixed model analysis that are further explained in the Results section.

Effects on pupal biomass

Egg induction resulted in a lower pupal mass ($F_{1,4} = 26.76$, $P < 0.001$, Fig. 1b, Table S3). The interaction between treatment and plant species was not significant ($F_{1,4} = 1.54$, $P = 0.18$). Only when the effect of egg induction was analysed for each of the species separately, species-specific effects were revealed; egg induction affected pupal mass in *B. nigra, B. oleracea,* and *S. arvensis,* but not in *M. moricandioides* and *M. arvensis* (Table S3). Moreover, plant species itself also influenced pupal mass; which was higher on *S. arvensis* and *B. nigra* plants compared to *M. arvensis, M. moricandioides,* and *B. oleracea* (Fig. 1b, Table S3). Egg-induced HR-like necrosis had no effect on the pupal mass of *P. brassicae* that had been feeding on eggs(+) *B. nigra* ($F_{1,1} = 2.85$, $P = 0.09$).

Effects on egg to pupa development time

Egg induction extended the larva-to-pupa development time of *P. brassicae* feeding on these plants ($F_{1,4} = 28.81$, $P < 0.001$, Fig. 1c, Table S4). The interaction between development time and treatment was not significant ($F_{1,4} = 0.99$, $P = 0.41$). Similar as for pupal mass, species-specific effects were only revealed when statistical analyses were performed for each plant species separately; egg induction affected development time in *B. nigra, B. oleracea,* and *S. arvensis,* but not in the two *Moricandia* species (Table S4). Moreover, plant species itself also influenced development time; which was longer on *M. arvensis,* and *M. moricandioides* compared to *S. arvensis* and *B. nigra* and *B. oleracea* (Fig. 1c, Table S4). HR had no effect on the egg-to-pupa development time of *P. brassicae* growing on *B. nigra* ($F_{1,1} = 2.63$, $P = 0.10$).

Discussion

Our results support previous findings that early non-feeding life stages of herbivores such as eggs can change plant quality. Egg-induced negative changes in plant quality were shown in most of the tested host-plant species and these effects were most pronounced during early larval development, but still, albeit to a lesser extent, affected pupal mass and larva-to-pupa development time. Thus, we show that this plant-mediated negative effect of egg deposition is not restricted to *B. nigra* (Pashalidou *et al.*, 2013), but is also found in other wild brassicaceous species.

Our results corroborate those of Geiselhardt *et al.* (2013), who investigated the effects of egg induction on *A. thaliana*, on the subsequent development of *P. brassicae* caterpillars. Geiselhardt *et al.* (2013) found that caterpillars caused less feeding damage, weighed less, and suffered twice the level of mortality on plants previously infested with eggs, compared with caterpillars that developed on egg-free plants. Bruessow *et al.* (2010) have described contrasting results, where application of *P. brassicae* egg extract on *A. thaliana* had no effect on the biomass of *P. brassicae* caterpillars. Treatment with egg extract followed by caterpillar feeding suppressed the expression of genes that were induced in control plants not treated with the extract (Bruessow *et al.*, 2010). It has also been shown that egg deposition causes priming, i.e. the plants activate their responses more rapidly in response to a new stress, e.g. feeding by caterpillars (Kim *et al.*, 2012). Kim *et al.* (2012) reported priming in tomato plants in terms of induction of jasmonic acid, a phytohormone playing an important role in the regulation of induced plant defences, with a concomitant increase in *PIN1* gene transcripts. It remains to be elucidated which mechanisms underlie the egg-induced resistance effects reported here and whether the same mechanisms are triggered in each of the plant species.

In this study, we have compared the effect of induction by *P. brassicae* eggs on plant quality in several wild plant species belonging to the Brassicaceae to reveal if these effects are common within this plant family. Our results show that the plant species differ in the extent to which egg induction affects plant quality and the subsequent development of the caterpillar and pupal stages. There were no plant-mediated effects on *P. brassicae* when developing on *M. arvensis* and only effects on early larval development when caterpillars were feeding on egg-induced *M. moricandioides* plants (based on within-species statistical analyses). A plausible explanation for these results could be that *M. arvensis* and *M. moricandioides* represent host plants of poorer quality for *P. brassicae* compared to e.g. *B. nigra* and *S. arvensis*. Thus, this low plant quality may over-rule the potential effect of egg induction. Moreover, a recent study reported that the main herbivores of *Moricandia* species are large grazers such as sheep and goats (Gómez, 1996). Although *P. brassicae* is also a common insect herbivore on these species, Gómez (1996) claimed that the defoliation of the plants due to the grazers is so strong that any potential selection exerted by *P. brassicae* would be cancelled out by the more intense herbivory of the grazers (Gómez, 1996). Considering that the plant species in our study vary in several traits (annual versus perennial, size, morphology) and the fact that they grow in different habitats, selection for egg induction may not be the same.

All plant species included in this study are natural host plants of *P. brassicae* (Gómez, 1996; Gols *et al.*, 2008; Fei *et al.*, 2014). *Pieris brassicae* is a voracious herbivore that can have a significant impact on plant survival and fitness of the annual *B. nigra* (Smallegange *et al.*, 2007). Therefore, early recognition of infestation by herbivores, i.e. already in the egg stage, followed by a response that negatively influences development of the larvae hatching from these eggs, may reduce damage levels and potentially enhance plant fitness (Pashalidou *et al.*, 2013). Other studies showed that egg induction influenced plant responses against herbivores, in different systems such as the sawfly *Diprion pini* and the pine *P. sylvestris* (Beyaert *et al.*, 2011) and tomato (*Solanum lycopersicum*) – tomato fruitworm moth (*Helicoverpa zea*) (Kim *et al.*, 2012). Thus, plant responses to eggs may have evolved as an effective protective measurement against herbivory, as they influence herbivore performance (Kim & Felton, 2013).

The consequences of egg deposition for plant quality are clearly not limited to the egg stage, because egg induction affected the performance of larval stages of *P. brassicae* (this study; Pashalidou *et al.*, 2013). Therefore, when studying food plant quality for insect herbivores, it is important to follow the insect herbivore until it has completed its immature development. Other parameters related to the caterpillar and pupal development may also be influenced by egg induction, such as larval mortality, adult weight, and adult fecundity, but these were not included in this study.

Although egg induction significantly affected larval and pupal development of *P. brassicae*, plant quality differences were most pronounced at the species level. Larval and pupal masses were lowest and the development time was longest in *B. oleracea* and the two *Moricandia* species and shortest for *P. brassicae*

developing on *B. nigra* and *S. arvensis*. Our results corroborate previous studies that indicate differences in performance of *P. brassicae* when developing on different brassicaceous species. *Pieris brassicae* larval and pupal performance varied between *B. nigra* and *Brassica juncea* (L.) plants. *Pieris brassicae* butterflies that developed on *B. juncea* were the heaviest, yet their developmental time was longer (Gols *et al.*, 2009). Another study showed that *P. brassicae* perform better on *B. nigra* compared to *Barbarea vulgaris* and *B. oleracea* (Sznajder & Harvey, 2003). Changes in plant quality owing to plant defensive chemistry can alter the structure and composition of their associated insect community (Bangert *et al.*, 2006; Johnson *et al.*, 2006; Poelman & Dicke, 2014). The same chemical compounds that plants use to deter generalist herbivores may be used by specialist herbivore species to recognise their food plants (Schoonhoven *et al.*, 2005). Many studies have shown that natural plant species can vary in their levels of secondary plant compounds that affect food plant quality for insect herbivores. In this study, we show that in addition to the relatively larger interspecific variation in plant quality, egg induction further alters plant quality.

We show that changes in plant quality induced by egg deposition can affect herbivore performance on different plant species. These results added extra information regarding induced plant resistance that includes the initial phase of plant colonisation. Future work should evaluate under field conditions whether *P. brassicae* shows oviposition preference for particular Brassicaceae species in relation to egg induction or differences in plant quality in general. It is currently unclear how strong these interactions are in natural environments and whether these traits are phylogenetically conserved within the Brassicaceae family. Moreover, molecular tools allow for the elucidation of the mechanism underlying egg induction and whether they are conserved across phylogenetically related plant species.

Supporting Information

Additional Supporting Information may be found in the online version of this article under the DOI reference:
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Table S1. Results from the mixed models testing the effects of egg deposition on larval biomass of the herbivore *P. brassicae* on different Brassicaceae species.

Table S2. Results from the linear mixed model (LMM) statistical analysis testing the effects of *P. brassicae* egg deposition on the caterpillar mass of the individuals hatching from these eggs for each of the plant species.

Table S3. Results from the linear mixed model (LMM) statistical analysis testing the effects of *P. brassicae* egg deposition on pupal mass of the individuals hatching from these eggs for each of the plant species.

Table S4. Results from the linear mixed model (LMM) statistical analysis testing the effects of *P. brassicae* egg deposition on developing time of individuals hatching from these eggs for each of the plant species.

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