Bulletin of Entomological Research (2012) **102**, 373–384
doi:10.1017/S0007485311000708

Developmental responses of the diamondback moth parasitoid *Diadegma semiclausum* (Hellén) (Hymenoptera: Ichneumonidae) to temperature and host plant species

L.M. Dosdall[1]*, M.P. Zalucki[2], J.A. Tansey[1] and M.J. Furlong[2]

[1]Department of Agricultural, Food and Nutritional Science, University of Alberta, Edmonton, AB T6G 2P5, Canada: [2]School of Biological Sciences, University of Queensland, St Lucia, QLD 4072, Australia

Abstract

Effects of constant rearing temperature and the plant species fed upon by its hosts were investigated for several developmental parameters of *Diadegma semiclausum* (Hellén), an important parasitoid of the diamondback moth, *Plutella xylostella* (L.). Temperature had highly significant effects on all developmental parameters measured, and effects were usually both linear and quadratic with increasing temperature. Host plant species, comprising *Brassica napus* L., *Brassica rapa* L. ssp. *pekinensis* and *Brassica oleracea* L. var. *capitata*, also affected development of the parasitoid, and significant interactions were observed between plant species and rearing temperature for all developmental parameters measured. Development of *D. semiclausum* occurred successfully on all host plant species tested for the temperature range of 10 to 25°C. However, when its *P. xylostella* hosts consumed leaf tissue of *B. napus*, no specimens survived to pupate at 30°C, whilst pupation and adult eclosion occurred at 30°C on *B. rapa* ssp. *pekinensis* and *B. oleracea* var. capitata. At high ambient temperatures, such as those characteristic of tropical or subtropical regions (especially at low elevations) or regions that undergo temperature increases due to climate change, *P. xylostella* is predicted to occur at a higher range of temperatures than its biocontrol agent, *D. semiclausum*. Effects of high temperatures are expected to be more profound on the parasitoid for some host plants than others, with greater developmental limitations for the parasitoid on *B. napus* than on *B. rapa* or *B. oleracea*.

Keywords: *Plutella xylostella*, developmental biology, *Brassica napus*, *Brassica rapa*, *Brassica oleracea*, biological control, canola, cabbage

(Accepted 25 October 2011; First published online 30 November 2011)

Introduction

Understanding the responses of arthropod predators and parasitoids to temperature and other climatic factors can be crucial for facilitating biological control, whether using the introduction, conservation or augmentation approaches (Roy *et al.*, 2002). Natural enemies and their hosts or prey may differ

---

*Author for correspondence
Fax: 1-780-492-4265
E-mail: lloyd.dosdall@ualberta.ca

in how temperature affects their survival, development, movement and reproduction, and this can affect the degree of population control parasitoids and predators exert on pest species of herbivores. Temperature requirements may vary among species (e.g. Frazer & McGregor, 1992; Mbapila *et al.*, 2002) and populations (Gilbert, 1988; Lee & Elliott, 1998), and can interact with other ecological factors like food source (Gilbert & Raworth, 1996) and allelochemicals (Stamp & Osier, 1998). Distinct thermal requirements by natural enemies and the herbivores on which they feed can cause asynchrony in periods of activity, resulting in pest outbreaks or reductions in biological control (Read, 1962). Consequently, studies on the developmental rates of natural enemies and their hosts/prey at different temperatures are instrumental for predicting the efficiencies of biological control strategies.

The diamondback moth, *Plutella xylostella* (L.) (Lepidoptera: Plutellidae), is a serious pest of brassicaceous vegetable and oilseed crops and has a worldwide distribution (Talekar & Shelton, 1993). Thermal effects on its survival and developmental biology from egg to adult eclosion have been well studied over a wide range of both constant (4–40°C) and fluctuating temperatures (Liu *et al.*, 2002). Throughout its range, more than 135 species of parasitoids can attack various life stages of *P. xylostella* (Delvare, 2004); and among these, species of the genus *Diadegma* (Hymenoptera: Ichneumonidae) are the most diverse and important economically (Sarfraz *et al.*, 2005). In Australia, several predator and parasitoid species can contribute to the biological control of *P. xylostella*, but the larval parasitoid *Diadegma semiclausum* (Hellén) has been dominant both in key regions of vegetable production (Furlong *et al.*, 2004) and in crops of canola (Furlong *et al.*, 2008). *Diadegma semiclausum* is not native to the southern hemisphere but was introduced initially to New Zealand from the UK (Robertson, 1948), followed by subsequent releases and establishment in many Australasian regions, such as Malaysia (Ooi, 1980), Taiwan (Talekar & Yang, 1991), the Philippines (Poelking, 1992) and Australia (Wilson, 1960; Furlong *et al.*, 2004).

Several researchers have observed that *D. semiclausum* is more effective for controlling populations of *P. xylostella* in cooler highlands in Asia-Pacific regions than in the lowlands where *Cotesia vestalis* (Haliday) (Hymenoptera: Braconidae) is more effective (Talekar & Yang, 1991; Talekar & Shelton, 1993; Verkerk & Wright, 1997; Liu *et al.*, 2000; Saucke *et al.*, 2000). The inability of *D. semiclausum* to adequately control populations of *P. xylostella* in the hotter conditions at lower elevations has been attributed to a lack of tolerance to high temperature conditions (Talekar & Yang, 1991; Talekar & Shelton, 1993). The relationship between temperature and development of *D. semiclausum* on an unspecified cabbage cultivar was investigated by Yang *et al.* (1993), who determined that proportions of individuals that hatched, pupated and eclosed as adults declined as temperatures increased from 30 to 35°C. However, developmental parameters other than survival, percent emergence and time from egg to pupation were not measured, and developmental rate below 15°C was not investigated.

Plant species on which herbivorous insects feed can affect developmental parameters of their parasitoids, due to the nutritional composition of the diet of the host, the occurrence of allelochemicals in the host that can be detrimental to the parasitoid or possible interactions between nutrients and allelochemicals (Turlings & Benrey, 1998). Sarfraz *et al.* (2008) investigated *Diadegma insulare* (Cresson), a Neotropical congener of *D. semiclausum*, and found that pre-imaginal developmental time, pupal weight, adult longevity and wing area varied depending on the plant species and cultivar fed upon by *P. xylostella* hosts. However, it is not known whether developmental characteristics of *D. semiclausum* at a given temperature can be affected by the plant species fed upon by its host, or if interactions exist between temperature and host plant species. With few exceptions (e.g. Iheagwam, 1980; Tomkins *et al.*, 1989; Larsen *et al.*, 1990; Abdel-Baky, 2008), interactions between insect rearing temperature and host plant species have rarely been investigated, and never previously to our knowledge at the third trophic level. The objective of this study was to investigate effects of temperature on several developmental parameters of *D. semiclausum* when its *P. xylostella* hosts were reared on three different brassicaceous host plant species that comprise economically important crops grown within the geographical ranges of both the herbivore and parasitoid. The study was designed to test the hypotheses that, when reared on *P. xylostella*, developmental parameters of *D. semiclausum* are affected by both temperature and host plant species, and that parameters associated with species fitness indicate a decline in fitness at higher constant rearing temperatures.

Methods and materials

Insects and host plants

The study was conducted using laboratory colonies of *P. xylostella* and *D. semiclausum* and three host plant species in the Brassicaceae: Chinese cabbage (*Brassica rapa* L. ssp. *pekinensis* (Lour) Olsson) cv. Wombok, common cabbage (*Brassica oleracea* L. var. *capitata* cv. Warrior) and canola (*Brassica napus* L. cv. Thunder TT). Plants were grown in a glasshouse at the University of Queensland, St Lucia, QLD, Australia in 15-cm-diameter plastic pots using an organic potting medium treated with a slow release fertilizer (Osmocote [N:P:K, 16:35:10] Scotts Australia Pty Ltd, Baulkham Hills, NSW, Australia). Three- to four-week-old plants were used for all experiments.

Specimens of *D. semiclausum* and *P. xylostella* were collected initially from a commercial cabbage field near Gatton, QLD (27°33′S; 152°17′E) and maintained in a laboratory growth cabinet on cabbage and Chinese cabbage at 25 ± 0.5°C, a relative humidity of 70%, and photoperiod of 16 h L:8 h D. Although *D. semiclausum* can oviposit in all four larval instars of *P. xylostella* (Yang *et al.*, 1993), second instars were used for *D. semiclausum* oviposition in each of our experiments. Newly molted second-instar larvae of *P. xylostella* were obtained by placing a potted plant of *B. rapa* ssp. *pekinensis* in a cage with 20–30 mated females of *P. xylostella* within a growth cabinet (at 25 ± 0.5°C) in darkness for 6–8 h for oviposition. Adult moths were then removed, and the plant was maintained at a constant temperature of 25°C for eight days until second-instar larvae emerged from their leaf mines. Approximately 60 to 80 second-instar *P. xylostella* larvae were then removed, placed into a Petri dish (9-cm-diameter) with moistened filter paper and a fresh leaf of the host plant species being evaluated. Six to eight mated females of *D. semiclausum* were then placed in the Petri dish for 6–8 h for parasitization. Mated females were obtained by transferring newly eclosed *D. semiclausum* females from the laboratory colony to small cages (approximately 30 × 30 × 30 cm) along with an equivalent number of males. Wasps were held for 2–3 days and provided *ad libitum* with water and honey, which was administered via cotton placed into a small test tube.

Following parasitization, the wasps were removed and larvae of *P. xylostella* were placed in Petri dishes (5-cm-diameter), with each dish containing a single larva and a filter paper moistened with distilled water. Fresh, excised leaf tissue of the host plant being evaluated was added and replaced daily, to enable each larval specimen to feed *ad libitum*.

Petri dishes with parasitized *P. xylostella* larvae and excised leaf tissue of *B. rapa* ssp. *pekinensis* were incubated at constant temperatures of 10, 15, 20, 23, 25, 28 and 30°C. Dishes with larvae and excised leaf tissue of *B. oleracea* var. *capitata* were incubated at 10, 15, 20, 23, 25 and 30°C, and dishes with larvae and excised leaf tissue of *B. napus* were incubated at 10, 15, 20, 25 and 30°C.

Parameters measured

Developmental times of *D. semiclausum* from egg to pupa were recorded for each replicate specimen. Pupae were removed within 12 h of pupation, weighed using a Sartorius Supermicro scale (Sartorius Inc., Edgewood, NY, USA) and returned to their respective containers until adult eclosion. Developmental times from pupa to adult emergence were recorded. Newly eclosed adults were maintained in sealed petri dishes with moistened filter paper but without food and returned to the controlled environment chambers to be held at the temperatures at which they were reared. Days from eclosion to death were recorded. After adult specimens died, they were held in labeled containers and allowed to dry; adult dry weights were recorded 7–10 days later. At this time, one forewing, a hindwing and a hind tibia were dissected from each specimen and photographed using a Dino-Lite Digital Microscope. DinoCapture software was used to determine tibia length, forewing length and hindwing length. The digital photographic images of the wings for each specimen were then imported to Image J software (National Institutes of Health, Bethesda, MD, USA) to quantify the areas of each according to the method of Sarfraz *et al*. (2007).

The measured parameters were selected for their known or predicted importance for indicating fitness: more rapid developmental times can enable parasitoids to avoid high mortality levels when fluctuations occur in host densities (Hackett-Jones *et al*., 2011), greater pupal and adult mass and longer-lived adults often indicate greater reproductive potential (e.g. Honek, 1993; Godfray, 1994; Schmid-Hempel & Schmid-Hempel, 1996; West *et al*., 1996), and larger wing areas and tibiae are generally positively correlated with fitness (Bethke *et al*., 1991; Sagarra *et al*., 2001; Salvo & Valladares, 2002).

Data analyses

Because *D. semiclausum* frequently has a male-biased sex ratio (Yang *et al*., 1993; Khatri *et al*., 2008), comparatively small numbers of replicate females were obtained, especially at temperature extremes; consequently, only data from males were used in our analyses. The effect of temperature for each developmental parameter was determined for each constant rearing temperature for each of the three host plant species using PROC MIXED of SAS (SAS Institute, 2005). All factors were considered fixed, and differences between temperatures for each host plant species were assessed using the LSMEANS statement with the PDIFF option in PROC MIXED.

Effects of host plant species, temperature, and interactions between host plant species and temperature were determined for all constant rearing temperatures common to all plant species and for which survival of *D. semiclausum* from egg to pupa occurred: 10, 15, 20 and 25°C. Data were subjected to analysis of variance using PROC MIXED of SAS, with all factors considered as fixed effects (SAS Institute, 2005). PROC MIXED was selected because it can better accommodate unbalanced data than PROC GLM (Yang, 2010). Differences between temperatures for each host plant species were assessed using the LSMEANS statement with the PDIFF option in PROC MIXED. Correlations were assessed among forewing area, hindwing area, tibia length and adult and pupal mass using PROC CORR of SAS. A Bonferroni correction was performed for pair-wise comparisons (the ADJUST = BON associated with the LSMEANS statement) to address potential correlations among adult and pupal mass. Data were distributed normally for all parameters except development time from egg to pupa, development time from egg to adult eclosion and longevity without food. Rank transformations were performed for data for those parameters not normally distributed according to Canover & Iman (1981), and data were subsequently analyzed with PROC MIXED. There are some concerns regarding inflation of Type I errors using this technique, when strong correlation exists between pre-test and post-test scores (Blair & Higgins, 1985). To address these concerns, a Bonferroni correction was performed for pair-wise comparisons.

Stepwise multiple regression analysis was performed for pupal and adult mass at each constant rearing temperature for each of the three host plant species using SAS PROC REG with the stepwise selection option (SAS Institute, 2005). Temperature and a variable created to represent the quadratic of temperature were evaluated as the independent variables with a developmental parameter as the dependent variable. A value of $\alpha \leq 0.05$ was required to retain parameters in the model. The main effect of thermal regime was decomposed to linear and quadratic effects to assess the trends of *D. semiclausum* development at various constant temperatures. This analysis helped facilitate identification of optimal and suboptimal temperature requirements for *D. semiclausum* because arthropod developmental rate is generally linear at moderate or optimal temperatures but curvilinear near the temperature extremes for a species (Wagner *et al*., 1984).

Days from oviposition to pupation, oviposition to eclosion and days to death following eclosion were evaluated for each temperature and host plant combination using the logistic regression model

$$P = \left(1 + e^{-(a+bT)}\right)^{-1} \tag{1}$$

(as per McClay & Hughes, 2007) where P represents the proportion of *D. semiclausum* pupating, eclosing or dying, T is time in days, and a and b are temperature-dependent parameters. The parameters a and b were fitted using the logistic regression procedure, specifying the described model, using Statistix 9.0 (Analytical Software, Tallahassee, FL, USA). These parameters were used to develop estimates of time (days) for 25% ($T_{0.25}$), 50% ($T_{0.50}$), 75% ($T_{0.75}$) and 100% ($T_{1.00}$) of *D. semiclausum* to pupate, eclose and die at each temperature and associated with each host plant. Death was restricted to a two-day period on Chinese cabbage at 15 and 25°C; therefore, days to death were transformed from 4.0 to 4.1 days for one of the 15 *D. semiclausum* specimens that died on the fourth day

Table 1. Results of analysis of variance for several developmental parameters of the parasitoid *Diadegma semiclausum* when its *Plutella xylostella* hosts were reared on different brassicaceous host plants at various constant temperatures. Analysis was performed for combined data of all host plant species (*Brassica rapa* ssp. *pekinensis*, *Brassica oleracea* var. *capitata*, and *Brassica napus*) when larvae were reared at temperatures of 10, 15, 20 and 25°C.

Developmental parameter	Plant species			Temperature			Plant × temperature		
	df	F	*P*	df	F	*P*	df	F	*P*
Pupal mass	2, 333	21.71	<0.001	3, 333	52.89	<0.001	6, 333	6.23	<0.001
Adult dry mass	2, 267	5.54	0.004	3, 267	5.27	0.002	6, 267	2.85	0.011
Days, egg to pupa	2, 340	17.13	<0.001	3, 340	3636.41	<0.001	6, 340	57.39	<0.001
Days, egg to adult	2, 281	5.94	0.003	3, 281	1977.80	<0.001	6, 281	24.81	<0.001
Days, adult to death	2, 281	8.07	<0.001	3, 281	224.11	<0.001	6, 281	7	<0.001

and from 2.0 to 2.1 days for one of the nine *D. semiclausum* that died on the second day to allow fitting of logistic models to these data.

Results

Hindwing and forewing length were highly correlated ($R=0.890$; df = 260; $P<0.001$) as were hindwing length and area ($R=0.879$; df = 261; $P<0.001$) and forewing length and area ($R=0.897$; df = 267; $P<0.001$). Pupal and adult mass and hindwing length were also highly correlated ($R=0.654$; df = 255; $P<0.001$ and $R=0.776$; df = 268; $P<0.001$, respectively). Pupal and adult mass and tibial length were highly correlated ($R=0.587$; df = 265; $P<0.001$ and $R=0.633$; df = 272; $P<0.001$, respectively). Because forewing area, hindwing area, tibia length and adult mass are measures of the same fitness measure, body size, only effects of host plant species and temperature on pupal and adult masses were assessed and presented.

Host plant species fed upon by *P. xylostella* significantly affected several developmental parameters of *D. semiclausum*, including pupal weight, adult dry weight, developmental time from egg to pupa and from egg to adult, and longevity of adults held without food ($P<0.01$ for all parameters) (table 1). Rearing temperature significantly affected all developmental parameters measured ($P<0.01$ for all comparisons), and significant interactions between host plant species and constant rearing temperature were detected for all developmental parameters ($P<0.05$) (table 1).

Pupal weights of *D. semiclausum* reared on *P. xylostella* larvae that consumed *B. oleracea* var. *capitata* differed significantly between 20 and 23°C ($F_{1,110}=3.27$; $P=0.021$) but not between other incremental temperature increases ($P>0.05$ for all comparisons) (fig. 1). Specimens of *D. semiclausum* reared on *B. rapa* had significant reductions in pupal weight between 10 and 15°C ($F_{1,222}=3.31$; $P=0.023$), and between 20 and 23°C ($F_{1,222}=3.99$; $P=0.002$). Specimens reared on *B. napus* had significant reductions in pupal weight between 15 and 20°C ($F_{1,132}=5.79$; $P<0.001$) but not between other incremental temperature increases ($P>0.05$ for all comparisons) (fig. 1).

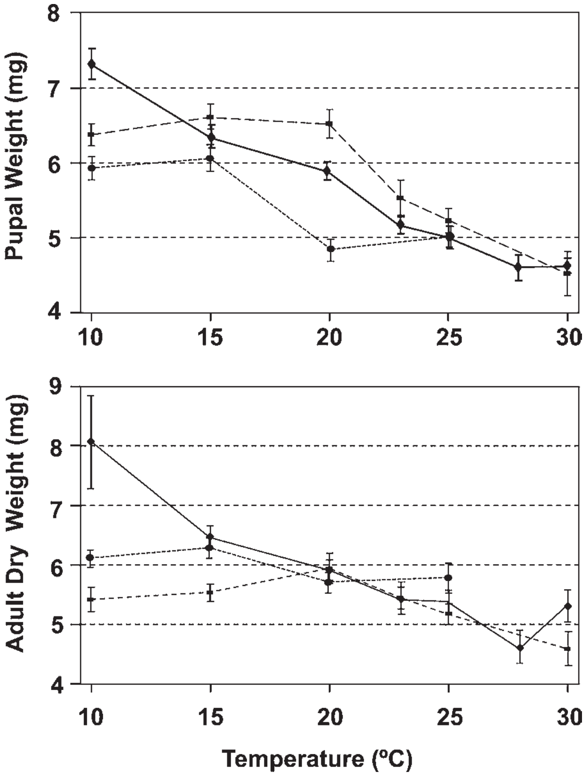

Fig. 1. Mean (±SE) pupal and adult dry weights of *Diadegma semiclausum* male specimens reared on reared on *Plutella xylostella* hosts at various constant temperatures on leaf tissue of *Brassica rapa*, *Brassica oleracea* and *Brassica napus* (—◆—, *Brassica rapa*; --■--, *Brassica oleracea*; --●--, *Brassica napus*).

Adult dry weights of *D. semiclausum* when its *P. xylostella* hosts were reared on *B. oleracea* did not differ significantly between any of the incremental temperature increases ($P>0.05$ for all comparisons) (fig. 1). However, adult dry weights differed significantly between constant rearing temperatures of 20 and 30°C ($F_{1,89}=3.96$; $P=0.002$). On *B. rapa*, adult dry weights of *D. semiclausum* differed significantly between 10 and 15°C ($F_{1,142}=2.09$; $P=0.0385$) and between 20 and 23°C ($F_{1,142}=2.20$; $P=0.0294$). Adult dry weights of *D. semiclausum* when *P. xylostella* fed upon *B. napus* differed significantly between 15 and 20°C ($F_{1,110}=3.22$; $P=0.010$) but not between other incremental temperature increases ($P>0.05$ for all comparisons) (fig. 1).

Development time of *D. semiclausum* from egg to pupation when its *P. xylostella* hosts were reared on *B. oleracea* declined significantly between all incremental rearing temperatures: 10–15°C ($F_{1,113}=7.68$; $P<0.0001$), 15–20°C ($F_{1,113}=7.39$; $P<0.0001$), 20–23°C ($F_{1,113}=8.43$; $P<0.0001$), 23–25°C ($F_{1,113}=3.12$; $P=0.0034$) and 25–30°C ($F_{1,113}=4.59$; $P=0.002$) (fig. 2). When host larvae were reared on *B. rapa*, reductions in time from egg to pupation were observed for temperatures

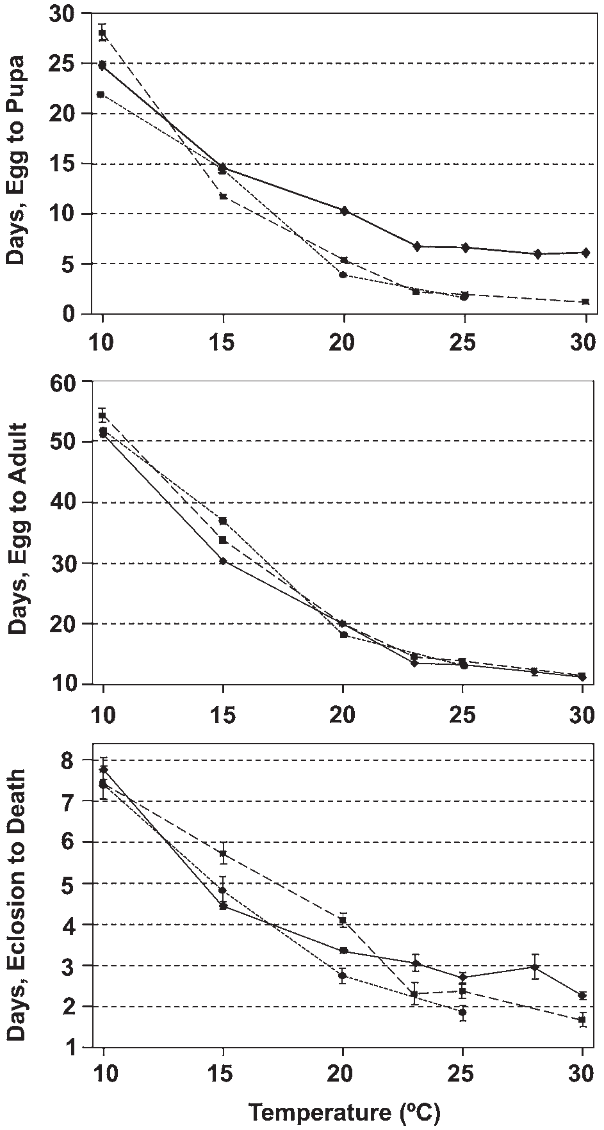

Fig. 2. Mean (±SE) development times from egg to pupa, egg to adult, and eclosion to death for *Diadegma semiclausum* male specimens reared on *Plutella xylostella* hosts at various constant temperatures on leaf tissue of *Brassica rapa*, *Brassica oleracea* and *Brassica napus* (—◆—, *Brassica rapa*; --■--, *Brassica oleracea*; --●--, *Brassica napus*).

between 10 and 15°C ($F_{1,232}=5.40$; $P<0.001$), 15 and 20°C ($F_{1,232}=5.29$; $P<0.001$), 20 and 23°C ($F_{1,232}=11.11$; $P<0.001$), and 25 and 28°C ($F_{1,232}=3.95$; $P=0.002$). When reared on *B. napus*, development time to pupation declined between 10 and 15°C ($F_{1,133}=16.62$; $P<0.001$), 15 and 20°C ($F_{1,133}=12.97$; $P<0.001$), and 20 and 25°C ($F_{1,133}=12.02$; $P<0.001$) (fig. 2).

Development time of *D. semiclausum* from egg to adult eclosion when its *P. xylostella* hosts were reared on *B. oleracea* declined for all incremental rearing temperatures: 10–15°C ($F_{1,95}=11.15$; $P<0.001$), 15–20°C ($F_{1,95}=9.91$; $P<0.001$), 20–23°C ($F_{1,95}=8.56$; $P<0.001$), 23–25°C ($F_{1,95}=4.41$; $P<0.001$) and 25–30°C ($F_{1,95}=6.81$; $P<0.0001$) (fig. 2). Similarly, on *B. rapa*, development time from egg to adult eclosion decreased from 10 to 15°C ($F_{1,151}=9.75$; $P<0.001$), 15 to 20°C ($F_{1,151}=10.47$; $P<0.001$), 20 to 23°C ($F_{1,151}=10.89$; $P<0.001$), 25 to 28°C ($F_{1,151}=3.79$; $P=0.0005$) and 28 to 30°C ($F_{1,151}=3.40$; $P=0.018$). For *P. xylostella* hosts reared on *B. napus*, days from egg to eclosion of *D. semiclausum* declined from 10 to 15°C ($F_{1,111}=17.20$; $P<0.001$), 15 to 20°C ($F_{1,111}=11.80$; $P<0.001$) and from 20 to 25°C ($F_{1,111}=7.94$; $P<0.001$) (fig. 2).

Days from adult eclosion to death of *D. semiclausum* when its *P. xylostella* hosts were reared on *B. oleracea* declined from 15 to 20°C ($F_{1,95}=4.24$; $P<0.001$) and 20 to 23°C ($F_{1,95}=4.36$; $P<0.001$) (fig. 2). When parasitized *P. xylostella* were reared on *B. rapa*, days from eclosion to death of *D. semiclausum* declined from 10 to 15°C ($F_{1,151}=9.75$; $P<0.1001$), 15 to 20°C ($F_{1,151}=10.47$; $P<0.001$), 20 to 23°C ($F_{1,151}=10.89$; $P<0.001$), 25 to 28°C ($F_{1,151}=3.79$; $P=0.005$) and from 28 to 30°C ($F_{1,151}=3.40$; $P=0.018$). Days from adult eclosion to death when *P. xylostella* hosts were reared on *B. napus* declined from 10 to 15°C ($F_{1,111}=6.74$; $P<0.001$) and 15 to 20°C ($F_{1,111}=7.27$; $P<0.001$) (fig. 2).

The significant interaction between plant species and temperature on pupal mass ($F_{6,333}=6.23$; $P<0.001$) (table 1) occurred between low and moderate temperatures. At 10°C the order of pupal mass was *B. rapa* > *B. oleracea* = *B. napus*, but at 20°C this changed to *B. oleracea* > *B. rapa* > *B. napus* (fig. 1). The interaction between plant species and temperature on adult dry weight ($F_{6,267}=2.85$; $P=0.011$) (table 1) was also detected between low and moderate temperatures with a change in dry weight from *B. rapa* = *B. napus* = *B. oleracea* at 10°C to *B. oleracea* = *B. rapa* > *B. napus* at 20°C (fig. 1).

The significant interaction between plant species and temperature on developmental time from egg to pupa ($F_{6,340}=57.39$; $P<0.001$) (table 1) was evident between 10 and 15°C, and between 15 and 20°C (fig. 2). At 10°C the order of plant species for time to pupation was *B. oleracea* > *B. rapa* > *B. napus*, but at 15°C this changed to *B. napus* > *B. oleracea* = *B. rapa*. At 20°C the order was *B. rapa* > *B. oleracea* > *B. napus*. Similarly, developmental time from egg to adult also had significant interactions ($F_{6,281}=24.81$; $P<0.001$) (table 1) between 10 and 15°C and between 15 and 20°C. At 10°C developmental time of *D. semiclausum* reared on *P. xylostella* larvae that consumed *B. oleracea* was similar to that of *B. napus* and *B. rapa*, but at 15°C the order of days from egg to adult eclosion was *B. napus* > *B. oleracea* > *B. rapa*. At 20°C the order was *B. rapa* and *B. oleracea* > *B. napus* (fig. 2).

Days from adult eclosion to death of *D. semiclausum* also had a significant interaction of plant species by temperature ($F_{6,281}=7.46$; $P<0.001$) (table 1) (fig. 2). At 15°C days to death for wasp specimens reared on *P. xylostella* hosts that fed on *B. rapa* significantly exceeded mortality times for *B. napus* and *B. oleracea*. At 20°C this order had changed to *B. oleracea* > *B. rapa* = *B. napus*, and at 25°C days to death for parasitoids reared on larvae that consumed *B. rapa*, *B. oleracea* and *B. napus* were similar (fig. 2).

Stepwise multiple regression analysis of the various developmental parameters for *D. semiclausum* when its *P. xylostella* hosts were reared on leaf tissue of *B. rapa* identified significant linear decreases in pupal mass (M_P) with temperature (T): $M_P = -1.29\text{E}-4(T)+0.008$. A decrease in adult mass (M_A) with the quadratic of temperature was also detected for this host plant: $M_A = -1.26\text{E}-7(T^2)+6.28\text{E}-4$. A peak in pupal mass near 14°C was detected for parasitoids from *P. xylostella* reared on *B. oleracea*: $M_P = 2.17\text{E}-4(T)+-7.99\text{E}-6(T^2)+0.005$. Adult parasitoids from *P. xylostella* reared on this

Table 2. Results of stepwise multiple regression analysis to determine pupal and adult mass (dependent variables) of the parasitoid *Diadegma semiclausum* when its *Plutella xylostella* hosts were reared on different brassicaceous host plants at various constant temperatures.

Plutella xylostella Host plant	Variable	Estimate	Partial R^2	Model R^2	F	P
Brassica rapa ssp. *pekinensis*	**Pupal mass (g)**					
	Intercept	0.008			2368.4	< 0.001
	Temperature (°C)	− 1.29E − 4	0.562	0.562	291.75	< 0.001
	Adult mass (g)					
	Intercept	6.28E − 4			1553.0	< 0.001
	(Temperature (°C))^2	− 1.26E − 7	0.114	0.114	18.85	< 0.001
Brassica oleracea var. *capitata*	**Pupal mass (g)**					
	Intercept	0.005			44.33	< 0.001
	Temperature (°C)	2.17E − 4	0.037	0.037	6.92	0.010
	(Temperature (°C))^2	− 7.99E − 6	0.363	0.400	65.04	< 0.001
	Adult mass (g)					
	Intercept	3.68E − 4			21.01	< 0.001
	Temperature (°C)	2.38E − 5	0.068	0.068	7.24	0.009
	(Temperature (°C))^2	− 6.96E − 7	0.068	0.136	6.74	0.011
Brassica napus	**Pupal mass (g)**					
	Intercept	0.007			1068.5	< 0.001
	Temperature (°C)	− 8.70E − 5	0.282	0.282	52.73	< 0.001
	Adult mass (g)					
	Intercept	6.02E − 4			1177.6	< 0.001
	(Temperature (°C))^2	− 1.39E − 7	0.063	0.063	7.56	0.007

host plant also demonstrated a peak in mass near 18°C: $M_A = 2.38E-5(T) + -6.96E-7(T^2) + 3.68E-4$. A linear decrease in pupal mass with temperature, and a decrease in adult mass with the quadratic of temperature were detected for parasitoids from *P. xylostella* reared on *B. napus:* $M_P = -8.70E-4(T) + 0.007$ and $M_A = -1.39E-7(T^2) + 6.02E-4$, respectively (table 2). For *B. rapa*, the model explained little of the variation in the data for adult dry weight ($R^2 = 0.11$; df = 148), but explained much of the variation for pupal weight ($R^2 = 0.56$; df = 228). For *B. oleracea* and *B. napus*, the models developed for the relationship of temperature and pupal mass also accounted for more variation ($R^2 = 0.40$; df = 115 and $R^2 = 0.28$; df = 135, respectively) than the models developed for adult mass ($R^2 = 0.14$; df = 94; and $R^2 = 0.06$; df = 113, respectively) (table 2).

Modeling of times to pupation, eclosion and death associated with different plant species and temperatures by logistic regression indicated that the sigmoidal patterns effectively described the developmental data; R^2 values ranged between 0.98 and 1.00 (fig. 3). At 10°C estimated requirements for development from egg to pupation ranged from 21.9 (*B. napus*) to 25.0 (*B. oleracea*) days for 25% of the population and from 28.6 to 44.5 days for 100% of the population on *B. napus* and *B. oleracea*, respectively (table 3). At 25°C days to pupation ranged from 5.2 (*B. napus*) to 5.7 (*B. oleracea*) for 25% of the population and from 9.9 (*B. rapa*) to 13.8 (*B. napus*) days for 100% of individuals (table 3).

Days from egg to adult eclosion at 10°C required 49.7 (*B. rapa*) to 50.5 (*B. napus*) days for 25% of the population and 60.7 (*B. napus*) to 73.8 (*B. oleracea*) days for 100% of *D. semiclausum* individuals (table 4). At 25°C this range declined to 12.3 (*B. napus*) to 12.4 (*B. rapa*) days for 25% of the population and 16.3 (*B. rapa*) to 26.8 (*B. oleracea*) days for 100% (table 4).

Days from adult eclosion to death for specimens reared at 10°C ranged from 4.6 (*B. rapa*) to 5.5 (*B. napus*) days for 25% of the population to 12.9 (*B. rapa*) to 14.8 (*B. oleracea*) days for 100% (table 5). At 25°C this range declined to 1.0 (*B. napus*) to 1.6 (*B. rapa*) days for 25% of individuals to 3.7 (*B. rapa*) to 8.0 (*B. oleracea*) days for 100% (table 5).

Discussion

Sustainable production of canola in Australia and brassicaceous vegetables in Australia and other Asia-Pacific regions requires control of diamondback moth with its natural enemies, especially *D. semiclausum*. We determined that temperature and host plant species differentially affected various developmental parameters of *D. semiclausum* and that interactions between temperature and host plant species occurred for all developmental parameters measured. Our hypothesis that parameters associated with species fitness decline at higher temperatures was validated for pupal and adult dry weights, but developmental times to pupa and adult eclosion were most rapid at higher rearing temperatures (figs 1 and 2). The ability of *P. xylostella* to complete development at a wider range of temperatures than its principal parasitoid could explain the greater effectiveness of *D. semiclausum* as a biological control agent at cooler, higher elevations of Asia-Pacific regions. Our results, indicating no complete development of *D. semiclausum* at 30°C when larvae of its host consumed *B. napus* but not *B. rapa* and *B. oleracea*, suggest that *D. semiclausum* may be a more effective biocontrol agent for crops of common cabbage and Chinese cabbage than canola.

Global temperatures have increased 0.7°C in the last century (Rosenzweig *et al.*, 2000), and conservative scenarios of current and future greenhouse gas emissions suggest that temperatures will increase by 1.4 to 5.8°C over the next century (Cohen & Miller, 2001; Karl & Trenbeth, 2003). Increases in global temperatures may affect insect populations by lengthening the growing season, altering emergence patterns, increasing rates of growth and development, and altering geographical distribution patterns (Porter *et al.*, 1991; Olfert & Weiss, 2006; Sutherst *et al.*, 2011). In Australia, climate change projections for 2050 suggest that low planetary greenhouse

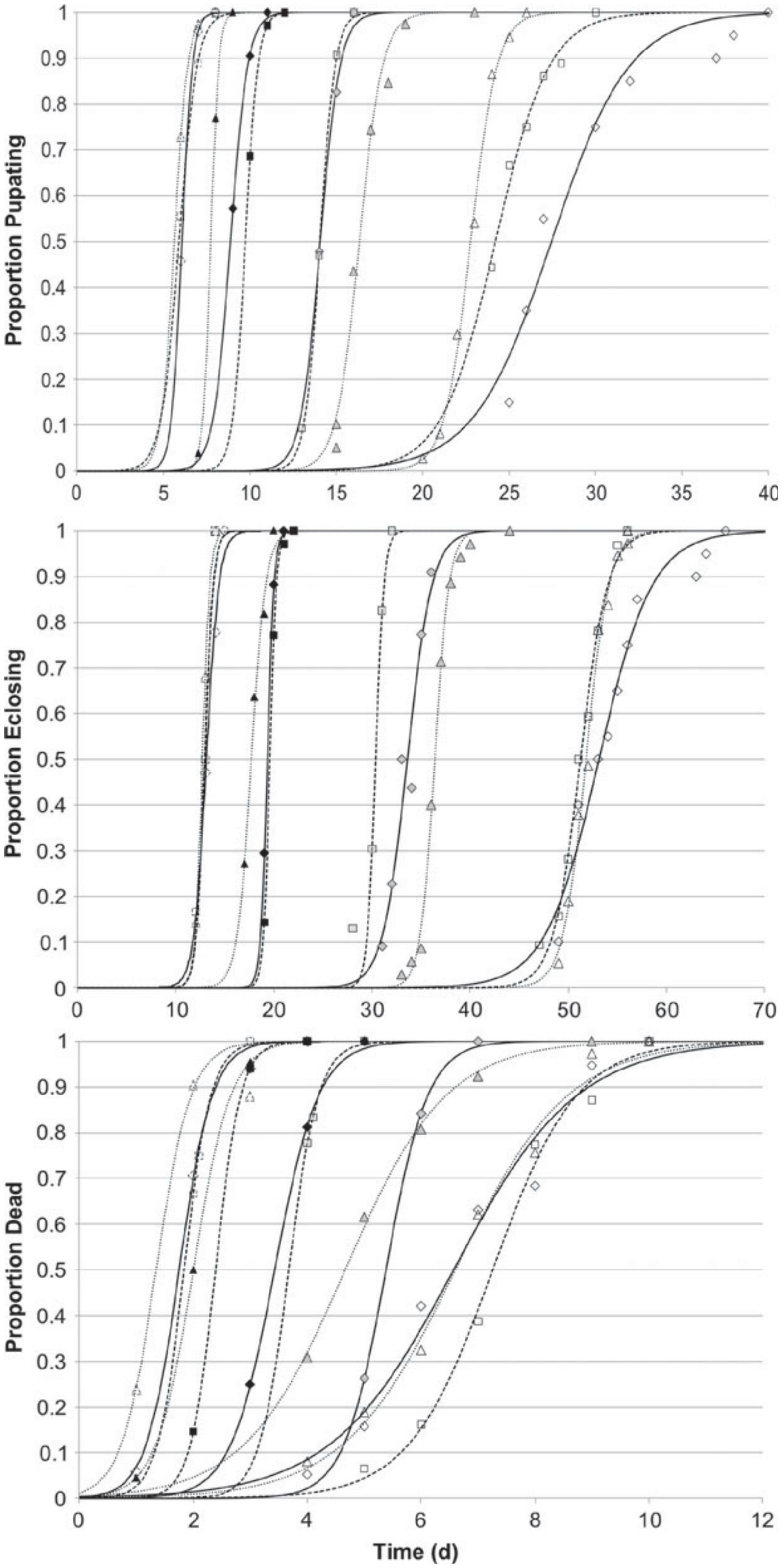

Fig. 3. Proportions of *Diadegma semiclausum* specimens pupating, eclosing and dead predicted with logistic analysis for various constant temperatures on leaf tissues of *Brassica rapa*, *Brassica oleracea* and *Brassica napus* (◊, *B. oleracea* 10°C; △, *B. napus* 10°C; □, *B. rapa* 10°C; ◈, *B. oleracea* 15°C; ◭, *B. napus* 15°C; ▨, *B. rapa* 15°C; ♦, *B. oleracea* 20°C; ▲, *B. napus* 20°C; ■, *B. rapa* 20°C; ◇, *B. oleracea* 25°C; △, *B. napus* 25°C; □, *B. rapa* 25°C; ——, *B. oleracea*; ··········, *B. napus*; ------, *B. rapa*).

Table 3. Logistic model parameters *a* and *b* (see text for details) used to develop estimates of time (days) for 25% ($T_{25\%}$), 50% ($T_{50\%}$), 75% ($T_{75\%}$) and 100% ($T_{100\%}$) of *D. semiclausum* to pupate.

Temperature	Host plant	Days to pupation					
		a	*b*	$T_{25\%}$	$T_{50\%}$	$T_{75\%}$	$T_{100\%}$
10°C	*B. oleracea*	−12.22	0.45	25.0	27.5	27.5	44.5
	B. napus	−29.89	1.31	21.9	22.8	23.6	28.6
	B. rapa	−15.60	0.64	22.5	24.2	25.9	36.0
15°C	*B. oleracea*	−24.80	1.76	13.4	14.1	14.7	26.3
	B. napus	−24.45	1.50	15.6	16.3	17.1	30.7
	B. rapa	−32.28	2.30	13.6	14.0	14.5	23.4
20°C	*B. oleracea*	−17.86	2.02	8.3	8.9	9.4	19.5
	B. napus	−34.26	4.43	7.5	7.7	8.0	12.6
	B. rapa	−26.77	2.76	9.3	9.7	10.1	17.5
25°C	*B. oleracea*	−20.00	3.31	5.7	6.1	6.4	12.6
	B. napus	−14.78	2.63	5.2	5.6	6.1	13.8
	B. rapa	−11.32	1.92	5.3	5.9	6.5	9.9

Table 4. Logistic model parameters *a* and *b* (see text for details) used to develop estimates of time (days) for 25% ($T_{25\%}$), 50% ($T_{50\%}$), 75% ($T_{75\%}$) and 100% ($T_{100\%}$) of *D. semiclausum* to develop from egg to eclosion.

Temperature	Host plant	Days to eclosion					
		a	*b*	$T_{25\%}$	$T_{50\%}$	$T_{75\%}$	$T_{100\%}$
10°C	*B. oleracea*	−19.56	0.37	50.1	53.1	56.1	73.8
	B. napus	−44.32	0.86	50.5	51.8	53.1	60.7
	B. rapa	−36.72	0.72	49.7	51.2	52.8	61.9
15°C	*B. oleracea*	−26.73	0.80	32.2	33.6	34.9	60.5
	B. napus	−49.54	1.36	35.6	36.4	37.2	52.1
	B. rapa	−71.23	2.35	29.9	30.3	30.8	39.5
20°C	*B. oleracea*	−56.00	2.90	18.9	19.3	19.7	26.7
	B. napus	−24.33	1.38	16.9	17.7	18.5	33.3
	B. rapa	−58.44	2.98	19.2	19.6	20.0	26.8
25°C	*B. oleracea*	−20.61	1.57	12.4	13.1	13.8	26.8
	B. napus	−33.68	2.65	12.3	12.7	13.1	20.8
	B. rapa	−29.55	2.29	12.4	12.9	13.4	16.3

Table 5. Logistic model parameters *a* and *b* (see text for details) used to develop estimates of time (days) for 25% ($T_{25\%}$), 50% ($T_{50\%}$), 75% ($T_{75\%}$) and 100% ($T_{100\%}$) of *D. semiclausum* to die following adult eclosion.

Temperature	Host plant	Days to death					
		a	*b*	$T_{25\%}$	$T_{50\%}$	$T_{75\%}$	$T_{100\%}$
10°C	*B. oleracea*	−6.08	0.93	5.4	6.6	7.8	14.8
	B. napus	−6.70	1.02	5.5	6.6	7.7	14.1
	B. rapa	−9.85	1.36	4.6	7.2	8.1	12.9
15°C	*B. oleracea*	−14.65	2.72	5.0	5.4	5.8	7.4
	B. napus	−5.28	1.13	3.7	4.7	5.6	9.5
	B. rapa	−14.22	3.86	3.4	3.7	4.0	5.1
20°C	*B. oleracea*	−8.90	2.60	3.0	3.4	3.9	5.5
	B. napus	−6.09	3.05	1.6	2.0	2.4	3.8
	B. rapa	−10.82	4.53	2.2	2.4	2.6	3.6
25°C	*B. oleracea*	−6.08	3.46	1.4	1.8	2.1	8.0
	B. napus	−4.43	3.28	1.0	1.4	1.7	7.9
	B. rapa	−6.08	4.28	1.6	1.8	2.1	3.7

gas emissions will result in an average temperature increase of 1.2°C relative to 1990 temperatures, but with high emissions this increase could average 2.2°C (CSIRO, 2007). Precipitation is predicted to change little in northern areas of the country, but in the south precipitation is predicted to decrease along a gradient that ultimately reaches 5–7% (CSIRO, 2007). With more degree-days, multivoltine insects like *P. xylostella* and *D. semiclausum* could produce more generations annually, as has been predicted for diamondback moth and *D. insulare* in North America (Dosdall *et al.*, 2008). Perhaps more importantly, the synchrony between herbivores and their parasitoids could become uncoupled if temperature drives species phenologies in different directions (van den Putten *et al*., 2004; Hance *et al*., 2007). In the case of *P. xylostella* and *D. semiclausum*, increases in ambient temperatures appear more likely to negatively affect the parasitoid than its host. Liu *et al*. (2002) determined that *P. xylostella* developed successfully from egg to adult eclosion at constant temperatures as high as 32°C and at alternating temperatures as high as 38°C. However, this study and previous research by Yang *et al*. (1993) indicate that survival and development of *D. semiclausum* decline dramatically at constant temperatures near 30°C. It is possible, therefore, that one impact of climate change could be decoupling of the phenological synchrony of *P. xylostella* with *D. semiclausum* in some regions of Australia, leading to greater reliance on population control with insecticide applications. This scenario appears more likely in regions of canola production because of the inability of *D. semiclausum* to persist on this host at constant temperatures of 30°C.

Interactions between temperature and the host plant species fed upon by the *P. xylostella* hosts of *D. semiclausum* occurred most often at the low (10–15°C) and high (25–30°C) constant temperature extremes. For instance, pupal weight was highest for specimens reared on hosts feeding on *B. rapa* at 10°C, but at 20°C pupal weight was greater for *B. oleracea* (fig. 1). At 10°C development time from egg to pupation was slowest on *B. oleracea* than on other host plant species, but at 20°C and higher this development was most prolonged on *B. rapa* (fig. 2). Among the host plant species we investigated, pupal weight, adult dry weight and days from eclosion to death were greater on *B. rapa* at the lowest temperature (10°C) than for *B. oleracea* and *B. napus*. By contrast, some developmental parameters for *B. napus* were lower than for the other two host plants at 10°C (pupal weight, days from egg to pupation); moderate temperatures appeared to favor development on *B. oleracea* and *B. rapa*. These results indicate that developmental parameters of *D. semiclausum* at the thermal extremes cannot be considered indicative of performance at moderate temperatures on all host plant species.

The three host plants investigated in this study have distinct structural characteristics: *B. rapa* ssp. *pekinensis* and *B. oleracea* var. *capitata* are comparatively low to the ground with a compact growth habit, but *B. napus* is erect, more branched and much taller. Gols *et al*. (2005) found that the structure of vegetation on which *P. xylostella* larvae were feeding affected the host-finding efficiency of *D. semiclausum*. Foraging parasitoid females located host larvae more rapidly on small plants of *Sinapis alba* L. than on large plants, and Gols *et al*. (2005) proposed that this may be attributed to differences in the composition or quantity of volatile chemical compounds (especially glucosinolates) that affected attractiveness. Alternatively, this difference in host-finding efficiency may have resulted from plant architectural characteristics, since geometry can influence parasitoid movement, depending on the spatial scale at which foraging occurs (Andow & Prokrym, 1990; Coll & Bottrell, 1996). If the host-finding efficiency of *D. semiclausum* is reduced in taller, erect *B. napus* plants relative to more compact *B. oleracea* var. *capitata* or *B. rapa* ssp. *pekinensis* plants, as suggested by Gols *et al*. (2005), it may further contribute to reduced biocontrol of *P. xylostella* in canola crops.

In addition to structural/morphological influences, host plants can affect parasitoid development and fitness through differences in quality and genotype. Sarfraz *et al*. (2009) found that, when *D. insulare* were reared on *P. xylostella* hosts that fed upon high-quality well fertilized plants of *B. napus*, developmental rate was significantly faster than on plants grown without fertilizer or with fertilizer applied at low to moderate rates. Plant genotype can also affect parasitoid development. For example, developmental time from egg to adult of *D. insulare* was significantly faster when parasitized *P. xylostella* larvae were reared on two *B. napus* cultivars than on *B. oleracea*, *Brassica carinata* L. and *B. rapa* (Sarfraz *et al*., 2008). Glucosinolate content of host plants likely contributes to these differences. Gols *et al*. (2008) found that glucosinolate contents in leaves can vary substantially among various plant species and populations, as well as for the same plant species during different times of the year (Gols *et al*., 2007); this could explain, in part, differences in developmental times of parasitoids when their hosts are reared on certain host plants. Pereira *et al*. (2002) reported that glucosinolate content is influenced by cultivation temperature for *B. oleracea* var. *italica*; greatest total glucosinolate content occurred at 10°C and 30 to 35°C. The influence on our results of temperature on production of plant glucosinolates is unknown but suggests directions for further study. Further, our studies were conducted with excised leaf tissue, and developmental parameters on intact tissues should be investigated.

Plant genotype and morphology can affect not only developmental rate but also parasitism success. Talekar & Yang (1991) found that level of parasitism by *D. semiclausum* was greater when *P. xylostella* larvae were feeding on common cabbage than on cauliflower (*B. oleracea* var. *italica*), broccoli (*B. oleracea* var. *botrytis*) or Chinese cabbage. In our study, pupal weight of *D. semiclausum*, which is an important fitness correlate of parasitoids (Schmid-Hempel & Schmid-Hempel, 1996), was greater at most constant temperatures when its *P. xylostella* hosts were reared on cabbage than on Chinese cabbage, and lowest on canola (fig. 1). Because *D. semiclausum* prefers to conduct host-seeking activity on plants on which its offspring are largest and develop most rapidly (Gols *et al*., 2009), the fitness advantage gained by *D. semiclausum* when its *P. xylostella* hosts feed on cabbage in terms of pupal weight may be linked to the increased parasitism success reported by Talekar & Yang (1991).

Sex ratio of *D. semiclausum* was strongly male-biased in our study; when rearing data for all temperatures and host plants were combined, the ratio was 0.85 M:0.15 F. Male-biased sex ratios of this and other species of *Diadegma* have been reported previously in the literature. Yang *et al*. (1993) investigated temperature effects in a population of *D. semiclausum* from Taiwan and found that sex ratio remained near 1:1 when specimens were reared from 15 to 25°C; but at higher rearing temperatures, the ratio became strongly skewed toward males. In addition to temperature, plant species on which host insects feed affects sex ratio in *D. semiclausum* (Rossbach, 2005). However, parasitoid genotype, the presence of a bacterial symbiont and single-locus complementary sex determination could also be involved. Kenji *et al*. (2005) determined that sex ratios *D. semiclausum* varied depending on genotype of the parasitoid, and van Wilgenburg *et al*. (2006) noted that the presence of *Wolbachia* bacteria can affect sex determination in the Hymenoptera. Butcher *et al*. (2000) found that single-locus complementary sex determination occurs in the congeneric species, *Diadegma chrysostictos* (Gmelin), wherein diploid males develop from fertilized eggs homozygous at the sex locus. The occurrence of diploid males through this process, as well as by development of haploid males from unfertilized eggs, can cause male-biased sex ratios after several generations.

In summary, we have shown that temperature and host plant species differentially affect developmental parameters of the parasitoid *D. semiclausum*. The frequent interactions between temperature and host plant species have implications for biological control because parasitization of herbivore hosts should presumably increase for the parasitoids with greatest fitness; depending on temperature, this can vary among crop plants. The ability of its *P. xylostella* hosts to complete development at a wider range of temperatures than its principal parasitoid could explain the greater effectiveness of *D. semiclausum* as a biological control agent at cooler, higher elevations of Asia-Pacific regions. In Australia, the potential consequences of these results for biological control appear more serious for crops of canola grown in regions subjected to high temperatures during crop production. However, the ability of other important members of the *P. xylostella* parasitoid fauna to develop at higher temperatures should be investigated to better understand the potential consequences for crop production associated with climate change.

Acknowledgements

Funding for this project was provided by the Natural Sciences and Engineering Research Council of Canada, the University of Alberta, Edmonton, AB, Canada and the University of Queensland, St Lucia, QLD, Australia. We are grateful to K. Renwick for technical assistance.

References

Abdel-Baky, N.F. (2008) Impact of temperatures and plant species on the biological features of the castor bean whitefly *Trialeurodes ricini*. *Journal of Insect Science* **8**, 2–3.

Andow, D.A. & Prokrym, D.R. (1990) Plant structural complexity and host-finding by a parasitoid. *Oecologia* **82**, 162–165.

Bethke, J.A., Nuessly, G.S., Paine, T.D. & Redak, R.A. (1991) Effect of host insect-host plant associations on selected fitness components of *Encarsia formosa* (Gahan) (Hymenoptera: Aphelinidae). *Biological Control* **1**, 164–169.

Blair, R.C. & Higgins, J.J. (1985) A comparison of the power of the paired samples rank transform statistic to that of Wilcoxon's signed ranks statistic. *Journal of Educational and Behavioral Statistics* **10**, 368–383.

Butcher, R.D.J., Whitfield, W.G.F. & Hubbard, S.F. (2000) Single-locus complementary sex determination in *Diadegma chrysostictos* (Gmelin) (Hympenoptera: Ichneumonidae). *Journal of Heredity* **91**, 104–111.

Cohen, S. & Miller, K. (2001) North America. pp. 737–800 *in* McCarthy, J.J., Canziani, O.F., Leary, N.A., Dokken, D.J. & White, K.S. (*Eds*) *Climate Change 2001: Impacts, Adaptation and Vulnerability*. Cambridge, UK, Cambridge University Press.

Coll, M. & Bottrell, D.G. (1996) Movement of an insect parasitoid in simple and diverse plant assemblages. *Ecological Entomology* **21**, 141–149.

Conover, W.J. & Iman, R.L. (1981) Rank transformations as a bridge between parametric and nonparametric statistics. *American Statistician* **35**, 124–129.

CSIRO (Commonwealth Scientific and Industrial Research Organization) (2007) Climate change in Australia. Technical Report. Available online at http://www.climatechangeinaustralia.gov.au/technical_report.php (accessed 2 November 2011).

Delvare, G. (2004) The taxonomic status and role of Hymenoptera in biological control of DBM, *Plutella xylostella* (L.) (Lepidoptera: Plutellidae). pp. 17–49 *in* Kirk, A.A. & Bordat, D. *(Eds) Improving Biocontrol of* Plutella xylostella*: Proceedings of the International Symposium*, 21–24 October 2002, Montpellier, France.

Dosdall, L.M., Weiss, R.M., Olfert, O., Mason, P.G. & Soroka, J.J. (2008) Diamondback moth, *Plutella xylostella* (L.), as a pest of canola in Canada: Its historical impact on the crop and predicted effects of climate change on its pest status. pp. 112–121 *in* Shelton, A.M., Collins, H.L., Zhang, Y. & Wu Q. (*Eds*) *Diamondback Moth and Other Crucifer Pests: Proceedings of the Fifth International Workshop*. China Agricultural Science and Technology Press, Beijing, People's Republic of China.

Frazer, B.D. & McGregor, R.R. (1992) Temperature-dependent survival and hatching rate of eggs of seven species of Coccinellidae. *The Canadian Entomologist* **124**, 305–312.

Furlong, M.J., Zu-Hua, S., Yin-Quan, L., Shi-Jian, G., Yao-Bin, L., Shu-Sheng, L. & Zalucki, M. (2004) Experimental analysis of the influence of pest management practice on the efficacy of an endemic arthropod natural enemy complex of the diamondback moth. *Journal of Economic Entomology* **97**, 1814–1827.

Furlong, M.J., Spafford, H., Ridland, P.M., Endersby, N.M., Edwards, O.R., Baker, G.J., Keller, M.A. & Paull, C.A. (2008) Ecology of diamondback moth in Australian canola: Landscape perspectives and the implications for management. *Australian Journal of Experimental Agriculture* **48**, 1494–1505.

Gilbert, N. (1988) Control of fecundity in *Pieris rapae*. V. Comparisons between populations. *Journal of Animal Ecology* **57**, 395–410.

Gilbert, N. & Raworth, D.A. (1996) Insects and temperature, a general theory. *The Canadian Entomologist* **128**, 1–13.

Godfray, H.C.J. (1994) *Parasitoids: Behavioural and Evolutionary Biology*. Chichester, UK, Princeton University Press.

Gols, R., Bukovinszky, T., Hemerik, L., Harvey, J.A., van Lenteren, J.C. & Vet, L.E.M. (2005) Reduced foraging efficiency of a parasitoid under habitat complexity: Implications for population stability and species coexistence. *Journal of Animal Ecology* **74**, 1059–1068.

Gols, R., Raaijmakers, C.E., van Dam, N.M., Dicke, M., Bukovinszky, T. & Harvey, J.A. (2007) Temporal changes affect plant chemistry and tritrophic interactions. *Basic and Applied Ecology* **8**, 421–433.

Gols, R., Bukovinszky, T., van Dam, N.M., Dicke, M., Bullock, J. M. & Harvey, J.A. (2008) Performance of generalist and specialist herbivores and their endoparasitoids differs on cultivated and wild *Brassica* populations. *Journal of Chemical Ecology* **34**, 132–143.

Gols, R., van Dam, N.M., Raaijmakers, C.E., Dicke, M. & Harvey, J.A. (2009) Are population differences in plant quality reflected in the preference and performance of two endoparasitoid wasps? *Oikos* **118**, 733–743.

Hackett-Jones, E., White, A. & Cobbold, C.A. (2011) The evolution of developmental timing in natural enemy systems. *Journal of Theoretical Biology* **275**, 1–11.

Hance, T., van Baaren, J., Vernon, P. & Boivin, G. (2007) Impact of extreme temperatures on parasitoids in a climate change perspective. *Annual Review of Entomology* **52**, 107–126.

Honek, A. (1993) Intraspecific variation in body size and fecundity in insects: a general relationship. *Oikos* **66**, 483–492.

Iheagwam, E.U. (1980) Influence of host plant (*Brassica* species) and temperature on population increase of the cabbage whitefly *Aleyrodes brassicae*. *Annals of Applied Biology* **95**, 273–278.

Karl, T.R. & Trenbeth, K.E. (2003) Modern global climate changes. *Science* **302**, 1719–1723.

Kenji, T., Graham, W. & Mitsutaka, S. (2005) Trial for sex ratio improvement of *Diadegma semiclausum* by reintroducing New Zealand strain. *Annual Report of the Society of Plant Protection of North Japan* **56**, 160–162.

Khatri, D., Wang, Q. & He, X.Z. (2008) Development and reproduction of *Diadegma semiclausum* (Hymenoptera: Ichneumonidae) on diamondback moth, *Plutella xylostella* (Lepidoptera: Plutellidae). *New Zealand Plant Protection* **61**, 322–327.

Larsen, K.J., Madden, L.V. & Nault, L.R. (1990) Effect of temperature and host plant on the development of the blackfaced leaf hopper. *Entomologia Experimentalis et Applicata* **55**, 285–294.

Lee, J.H. & Elliott, N.C. (1998) Comparison of developmental responses to temperature in *Aphelinus asychis* (Walker) from two different geographic regions. *Southwestern Entomologist* **23**, 77–82.

Liu, S.-S., Wang, X.G., Guo, S.J., He, J.H. & Shi, Z.H. (2000) Seasonal abundance of the parasitoid complex associated with the diamondback moth, *Plutella xylostella* (Lepidoptera: Plutellidae) in Hangzhou, China. *Bulletin of Entomological Research* **90**, 221–231.

Liu, S.-S., Chen, F.-Z. & Zalucki, M.P. (2002) Development and survival of the diamondback moth (Lepidoptera: Plutellidae) at constant and alternating temperatures. *Environmental Entomology* **31**, 221–231.

Mbapila, J.C., Overholt, W.A. & Kayumbo, H.Y. (2002) Comparative development and population growth of an exotic stemborer, *Chilo partellus* (Swinhoe), and an ecologically similar congener, *C. orichalcociliellus* (Strand) (Lepidoptera: Crambidae). *Insect Science and its Application* **22**, 21–27.

McClay, A.S. & Hughes, R.B. (2007) Temperature and host plant effects on development and population growth of *Mecinus janthinus* (Coleoptera: Curculionidae), a biological control agent for invasive *Linaria* spp. *Biological Control* **40**, 405–410.

Olfert, O. & Weiss, R.M. (2006) Impact of climate change on potential distributions and relative abundances of *Oulema melanopus*, *Meligethes viridescens* and *Ceutorhynchus obstrictus* in Canada. *Agriculture, Ecosystems & Environment* **113**, 295–301.

Ooi, P.A.C. (1980) Laboratory studies of *Diadegma cerophagus* (Hymenoptera: Ichneumonidae), a parasite introduced to control *Plutella xylostella* (Lepidoptera: Yponomeutidae) in Malaysia. *Entomophaga* **25**, 249–259.

Pereira, F.M.V., Rosa, E., Fahey, J.W., Stephenson, K.K., Carvalho, R. & Aires, A. (2002) Influence of temperature and ontogeny on the levels of glucosinolates in broccoli (*Brassica oleracea* var. italica) sprouts and their effect on the induction of mammalian phase 2 enzymes. *Journal of Agricultural and Food Chemistry* **50**, 6239–6244.

Porter, J.H., Parry, M.L. & Carter, T.R. (1991) The potential effects of climatic change on agricultural insect pests. *Agricultural and Forest Meteorology* **57**, 221–240.

Poelking, A. (1992) Diamondback moth in the Philippines and its control with *Diadegma semiclausum*. pp. 271–278 *in* Talekar, N.S. *(Ed) Diamondback Moth and Other Crucifer Pests: Proceedings of the Second International Workshop*. Asian Vegetable Research and Development Center, Shanhua, Taiwan.

Read, D.C. (1962) Notes on the life history of *Aleochara bilineata* (Gyll.) (Coleoptera: Staphylinidae), and on its potential value as a control agent for the cabbage maggot, *Hylemya brassicae* (Bouché) (Diptera: Anthomyiidae). *The Canadian Entomologist* **94**, 417–424.

Robertson, P.L. (1948) *Eupteromalus* sp. as a hyperparasite. Some indication of its influence on the establishment of *Angitia cerophaga* in New Zealand. *New Zealand Journal of Science and Technology* **29**, 257–265.

Rosenzweig, C., Iglesias, A., Yang, X.B., Epstein, P.R. & Chivian, E. (2000) Climate Change and US Agriculture: The Impacts of Warming and Extreme Weather Events on Productivity, Plant Diseases and Pests. Harvard University, Cambridge, MA, USA, Center for Health and Global Environment.

Rossbach, A. (2005) Influence of the host shift of the diamondback moth, *Plutella xylostella* L. to peas on its parasitoids in Kenya. PhD thesis, Georg-August Universität, Göttingen, Germany.

Roy, M., Brodeur, J. & Cloutier, C. (2002) Relationship between temperature and development rate of *Stethorus punctillum* (Coleoptera: Coccinellidae) and its prey *Tetranychus mcdanieli* (Acarina: Tetranychidae). *Environmental Entomology* **31**, 177–187.

Sagarra, L.A., Vincent, C. & Stewart, R.K. (2001) Body size as an indicator of parasitoid quality in male and female *Anagyrus kamali* (Hymenoptera: Encyrtidae). *Bulletin of Entomological Research* **91**, 363–367.

Salvo, A. & Valladares, G. (2002) Plant-related intraspecific size variation in parasitoids (Hymenoptera: Parasitica) of a polyphagous leafminer (Diptera: Agromyzidae). *Environmental Entomology* **31**, 874–879.

Sarfraz, M., Keddie, B.A. & Dosdall, L.M. (2005) Biological control of the diamondback moth, *Plutella xylostella* (L.): A review. *Biocontrol Science and Technology* **15**, 763–789.

Sarfraz, M., Dosdall, L.M. & Keddie, B.A. (2007) Resistance of some cultivated Brassicaceae to infestations by *Plutella xylostella* (Lepidoptera: Plutellidae). *Journal of Economic Entomology* **100**, 215–224.

Sarfraz, M., Dosdall, L.M. & Keddie, B.A. (2008) Host plant genotype of the herbivore *Plutella xylostella* (Lepidoptera: Plutellidae) affects the performance of its parasitoid *Diadegma insulare* (Hymenoptera: Ichneumonidae). *Biological Control* **44**, 42–51.

Sarfraz, M., Dosdall, L.M. & Keddie, B.A. (2009) Host plant nutritional quality affects the performance of the parasitoid *Diadegma insulare*. *Biological Control* **51**, 34–41.

SAS Institute (2005) SAS version 9.1. SAS Institute Inc. Cary, NC, USA.

Saucke, H., Dori, F. & Schumutterer, H. (2000) Biological and integrated control of *Plutella xylostella* (Lep., Yponomeutidae) and *Crocidolomia pavonana* (Lep., Pyralidae) in *Brassica* crops in Papua New Guinea. *Biocontrol Science and Technology* **10**, 595–606.

Schmid-Hempel, R. & Schmid-Hempel, P. (1996) Host choice and fitness correlates for conopid flies parasitising bumblebees. *Oecologia* **107**, 71–78.

Stamp, N.E. & Osier, T.L. (1998) Response of five insect herbivores to multiple allelochemicals under fluctuating temperatures. *Entomologia Experimentalis et Applicata* **88**, 81–96.

Sutherst, R.W., Constable, F., Finlay, K.J., Harrington, R., Luck, J. & Zalucki, M.P. (2011) Adapting to crop pest and pathogen risks under a changing climate. *Interdisciplinary Reviews: Climate Change* **2**, 220–237.

Talekar, N.S. & Shelton, A.M. (1993) Biology, ecology and management of the diamondback moth. *Annual Review of Entomology* **38**, 275–301.

Talekar, N.S. & Yang, J.C. (1991) Characteristic of parasitism of diamondback moth by two larval parasites. *Entomophaga* **36**, 95–104.

Tomkins, A.R., Penman, D.R. & Chapman, R.B. (1989) Effect of temperature and host plant on development of three species of leafrollers (Lepidoptera: Tortricidae). *New Zealand Entomologist* **12**, 48–54.

Turlings, T.C.J. & Benrey, B. (1998) Effects of plant metabolites on the behavior and development of parasitic wasps. *Ecoscience* **5**, 321–333.

van den Putten, W.H., de Ruiterb, P.C., Bezemera, T.M., Harvey, J.A., Wassen, M. & Wolters, V. (2004) Trophic interactions in a changing world. *Basic and Applied Ecology* **5**, 487–494.

van Wilgenburg, E., Driessen, G. & Beukeboom, L.W. (2006) Single locus complementary sex determination in Hymenoptera: An "unintelligent" design? *Frontiers in Zoology* **3**, 1. Available online at http://www.frontiersinzoology.com/content/3/1/1 (accessed 2 November 2011).

Verkerk, R.H.J. & Wright, D.J. (1997) Field-based studies with the diamondback moth tritrophic system in Cameron Highlands of Malaysia: Implications for pest management. *International Journal of Pest Management* **43**, 27–33.

Wagner, T.L., Wu, H.-I., Sharpe, P.J.H., Schoolfield, R.M. & Coulson, R.N. (1984) Modeling insect development rates: A literature review and application of a biophysical model. *Annals of the Entomological Society of America* **77**, 208–225.

West, S.A., Flanagan, K.E. & Godfray, H.C.J. (1996) The relationship between parasitoid size and fitness in the field, a study of *Achrysocharoides zwoelferi* (Hymenoptera: Eulophidae). *Journal of Animal Ecology* **65**, 631–639.

Wilson, F. (1960) A review of the biological control of insects and weeds in Australia and Australian New Guinea. Technical Communication No 1. Commonwealth Institute of Biological Control, Ottawa, Canada, Commonwealth Agricultural Bureaux, UK.

Yang, R.-C. (2010) Towards understanding and use of mixed-model analysis of agricultural experiments. *Canadian Journal of Plant Science* **90**, 605–627.

Yang, Y.-C., Chu, Y.-I. & Talekar, N.S. (1993) Biological studies of *Diadegma semiclausum* (Hym., Ichneumonidae), a parasite of diamondback moth. *Entomophaga* **38**, 579–586.