Bottom-up and top-down effects in a tritrophic system: the population dynamics of *Plutella xylostella* (L.)–*Cotesia plutellae* (Kurdjumov) on different host plants

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Abstract. 1. The effects of host-plant resistance on the population dynamics of the Diamondback moth, *Plutella xylostella* L., and its solitary parasitoid, *Cotesia plutellae* (Kurdjumov), were studied in replicated time-series experiments.

2. Host-plant resistance did not affect the equilibrial abundance of the Diamondback moth, but it affected the dynamics of Diamondback moth populations.

3. The mean population size of Diamondback moth showed no significant difference between *Brassica rapa* (a susceptible host plant) and *Brassica napus* (a partially resistant host plant) either in the presence or absence of the parasitoid.

4. Time-series analysis suggests that the dynamics of Diamondback moth on *B. rapa* were underpinned by delayed density-dependent processes. In contrast, the dynamics of the moth on *B. napus* were influenced by a direct density-dependent process.

5. Although measures of short-term parasitism showed a significantly higher rate of parasitism by *C. plutellae* on Diamondback moth feeding on *B. napus* compared with *B. rapa*, this individual performance does not translate into differences in the population dynamics. Analysis shows no significant difference in the persistence time of the population-level interaction between the host and parasitoid on the two different host plants.

Key words. Density dependence, Diamondback moth, host-plant resistance, population dynamics, population persistence, time-series analysis.

Introduction

The importance of the role of multitrophic interactions and the regulatory effects of bottom-up vs. top-down forces on population abundance and distribution has been a controversial theme in ecology (Power, 1992). Despite the general acceptance of the influences of bottom-up and top-down forces on herbivore populations (Hartvigsen *et al.*, 1995; Hunter *et al.*, 1997; Gratton & Denno, 2003), these ecological processes are often considered to be specific to particular ecosystems (Power, 1992). For instance, top-down effects

are considered more influential in aquatic systems (Power *et al.*, 1996; Polis *et al.*, 1998). In contrast, the bottom-up effects of plants may be more effective in trophic interactions in terrestrial systems (Stiling & Rossi, 1997; Ostfeld & Keesing, 2000). For example, in a survey of the literature published between 1970 and 1994, Harrison and Cappuccino (1995) found that resources (bottom-up forces) were much more common as a regulating factor than natural enemies in a variety of different terrestrial systems.

The role of bottom-up effects and, in particular, food limitation in regulating insect populations is of prime importance (Bonsall & Eber, 2001; Umbanhowar & Hastings, 2002) as the population dynamics of both herbivore and herbivore–natural enemy interactions may be influenced by variation in host-plant characteristics (Hunter & Price, 1992; Godfray, 1994). For instance, variation in host-plant quality

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may affect the body size of herbivorous insects, which, in turn, can determine life-history parameters such as fecundity, longevity, and survival, all directly relevant to population dynamics (Bezemer & Jones, 1998; Bjorkman, 2000; de Bruyn *et al.*, 2002). Furthermore, the effects of resource variation, which impacts on the behaviour or the physiology of herbivores, may cascade up to the population dynamics of higher trophic levels due to significant influences on the fitness and performance (such as survival, development, size, longevity, fecundity, and sex ratio) of natural enemies (Moon *et al.*, 2000; Sumerford *et al.*, 2000; Teder & Tammaru, 2002).

It is now evident that both host-plant quality and quantity govern the pattern of spatial and temporal heterogeneity amongst herbivore populations (Hunter & Price, 1992). Furthermore, variation in host-plant quality and quantity can be influential in determining the core characteristics of populations (such as density and distribution in space and time) at higher trophic levels (Hunter & Price, 1992; Price & Hunter, 1995); however, variation in host-plant characteristics may have differential effects on a herbivore and its associated natural enemies (Teder & Tammaru, 2002). Consequently, understanding the relative contributions of bottom-up effects on consumer and natural enemy trophic levels will provide a more focused comprehension of multispecies insect population dynamics (Ohgushi, 1995).

In the past decade, the effects of host-plant resistance on higher trophic levels have received considerable attention (e.g. Kareiva & Sahakian, 1990; Reed *et al.*, 1992; Heinz & Zalom, 1996; Farid *et al.*, 1998a, b; Fuentes-Contreras & Niemeyer, 1998; Kennedy, 2003). Here, however, the objective is to explore the bottom-up effects of plant resistance on the dynamics of populations at higher trophic levels. In particular, the aim of this study is to test the effects of host-plant resistance on the population dynamics of a herbivore and its specialist parasitoid over several generations. Specifically, interest lies in determining the possible regulatory effect of different host-plant types on both the single-species (herbivore) interaction and the predator–prey interaction.

After introducing the system and methods used to investigate the population dynamics of a tritrophic interaction, it is shown that host-plant type does not affect the equilibrial abundance of an insect herbivore but does impact on the population dynamics of the herbivore. However, in the presence of a natural enemy, the underlying host-plant type has little impact on the persistence time of the whole system. The study concludes by discussing the possible ecological processes and mechanisms leading to these similarities and differences.

Materials and methods

To explore the impact of host-plant type on the dynamics of an insect herbivore–parasitoid interaction, a tritrophic laboratory system was developed. In particular, the system was composed of two host plants, *Brassica rapa* and *B. napus*, Diamondback moth, *Plutella xylostella* L. (Lepidoptera:

Yponomeutidae), and its larval solitary parasitoid, *Cotesia plutellae* (Kurdjumov) (Hymenoptera: Braconidae). This system was chosen for a number of reasons. First, it is has been shown that *B. rapa* (Plant Introduction 469895) and *B. napus* (Plant Introduction 470055) (North Central Regional Plant Introduction Station, Ames, Iowa) are susceptible and partially resistant to attack by *P. xylostella* (Ramachandran *et al.*, 1998). Second, there is considerable information available on the biology of Diamondback moth and *Cotesia plutellae* (Talekar & Shelton, 1993; Kawaguchi & Tanaka, 1999; Shi *et al.*, 2002). Finally, *P. xylostella* is a worldwide pest species of crucifers (Sivapragasam *et al.*, 1997) and understanding its population dynamics is central to developing an integrated management strategy for its control (Wright & Verkerk, 1995; Verkerk & Wright, 1996a; Schuler *et al.*, 2003).

Plant–insect rearing protocols

Brassica rapa and *B. napus* were grown organically under greenhouse conditions ($25 \pm 5\,^{\circ}$C; L:D 16:8 h). Diamondback moth (originally from the Philippines) and *Cotesia plutellae* were both obtained from Rothamsted Research (Harpenden, Herts, U.K.). Cultures of *P. xylostella* were maintained on 3–4-week-old *Brassica pekinensis* cv. Tip Top (Chiltern Seeds, Ulverston, U.K.) in ventilated Perspex oviposition cages ($35 \times 35 \times 35$ cm). Similarly, the cultures of *C. plutellae*, in turn, were maintained on *P. xylostella* larvae in ventilated Perspex oviposition cages ($45 \times 45 \times 45$ cm). Both cultures were reared in a standard constant environment ($25 \pm 2\,^{\circ}$C; $70 \pm 5\%$ RH; L:D 16:8 h).

Levels of parasitism

To test the hypothesis that parasitism by *C. plutellae* differs between Diamondback moth on partially resistant and susceptible host plants, *P. xylostella* larvae reared on the different host plants were exposed to attack by the parasitoid. In particular, Diamondback moth larvae were reared on 6-week-old host plants, *B. rapa* and *B. napus*, until the second instar. Ten 2-day-old second instar larvae were then transferred into a plastic Petri dish (5 cm in diameter) and a single, mated 2-day-old female wasp (reared from Diamondback moth feeding on *B. pekinensis*) was released into the dish. For each larval type (reared on partially resistant or susceptible host plants) two exposure treatments were undertaken: 1 h exposure to parasitism and 2 h exposure to parasitism. The exposure of the larvae to the parasitoid was performed in absence of the host plant to minimise any olfactory effects of the host plants on the parasitoid. All *P. xylostella* larvae were then reared on the leaves of the appropriate host plant until either the moths pupated or a parasitoid cocoon formed. Each treatment was replicated 10 times.

Population dynamics

To explore the hypothesis that differences in plant resistance affect the population dynamics of *P. xylostella* a long-term resource-limited population dynamic experiment was established using the two different host plants (*B. rapa* and *B. napus*) in the presence or absence of *C. plutellae*. The treatments were replicated four times in a randomised block design, and maintained under constant environmental conditions (28 ± 2 °C; 70 ± 10% RH; L:D 16:8 h). To start the experiment, one 5-week-old plant, six pairs (male and female) of newly emerged *P. xylostella* adults, and aqueous honey solution (35%) were placed in each cage (55 × 28 × 45 cm). A new plant of the same age was put in the cages every 4 days. Each plant was kept in the cage for 12 days (equal to the developmental period of *P. xylostella* and *C. plutellae* from adult to adult). This resource renewal regime ensured that there was a low probability of removing part of the population during plant replacement. The adult food supply (honey solution) was replaced every 48 h. After 5 weeks, when a population of *P. xylostella* with overlapping generations (all stages present) had established, two 2-day-old mated female *C. plutellae* were introduced to each cage (in parasitoid-present treatments only).

The trophic interactions between the host plant and *P. xylostella*, and tritrophic interactions between the host plant, *P. xylostella* and *C. plutellae* were monitored by weekly census counts of live adults, and the data used as a measure of abundance for the population dynamics. The experiment was run until 14 generations of *P. xylostella* were completed.

Statistical analyses

Differences in the levels of parasitism between the two host-plant types were analysed using standard logistic regression techniques (Crawley, 2002). The population dynamic experiments were analysed using a series of descriptive and detailed statistical techniques (Royama, 1992; Chatfield, 1996). Autocorrelation (ACF) and partial autocorrelation (PACF) functions were examined to identify potential patterns (trends, persistent effects of preceding densities, or random shocks) present in the time-series data (Tabachnick & Fidell, 2001). Moreover, the PACF values also indicate the time lags at which negative feedback may be operating (the order of density dependence). The significance of lagged densities in the ACFs and PACFs were tested with Bartlett's band ($\pm 2/\sqrt{n}$), where *n* is the length of time series (Royama, 1992; Chatfield, 1996; Crawley, 2002). To explore the role of density dependence on the interactions, the net reproductive rate of the Diamondback moth population was calculated as $R_t = \ln(N_{t+1}/N_t)$, where N_t and N_{t+1} are population abundance at time t and $t+1$, respectively. Density dependence processes were then detected by testing the relationship between R_t and (the natural log-transformed) population abundance at times t, $t-1$, and $t-2$. The most parsimonious linear autoregressive model was obtained by initially fitting the maximal model [$R_t \sim \ln(N_t) + \ln(N_{t-1}) + \ln(N_{t-2})$] and then removing non-significant terms through model simplification (Ylioja *et al.*, 1999; Crawley, 2002). All statistical analyses were completed in S-Plus 6.1 (Insightful Corp., Seattle).

Results

Levels of parasitism

There was a significantly different rate of parasitism (Fig. 1) by *C. plutellae* on *P. xylostella* reared on the two host plants (1-h exposure: *z*-value = −6.187, d.f. = 18, $P < 0.001$; 2-h exposure: *z*-value = −3.505, d.f. = 17, $P < 0.001$). The proportion of hosts on *B. napus* attacked by *C. plutellae* was significantly greater than for Diamondback moth reared on *B. rapa* (0.875 vs. 0.320 under 1-h exposure and 0.960 vs. 0.712 under 2-h exposure).

Population dynamics: the effects of host-plant resistance on the population dynamics of Diamondback moth

Descriptive analysis. In absence of the parasitoid, all four replicates of Diamondback moth on both host plants persisted throughout the 24 weeks of the experiment (Fig. 2). In general the pattern of fluctuations exhibited neither a noticeable trend, nor systematic changes with time. This indicates that the populations are statistically stationary and therefore possibly regulated around an equilibrial level. The mean number of Diamondback moth adults per week per cage on *B. rapa* varied from 92.4 to 122.8, and between 94.4 and 143.3 for Diamondback moth on *B. napus* (Table 1). Comparison of the two overall mean abundances
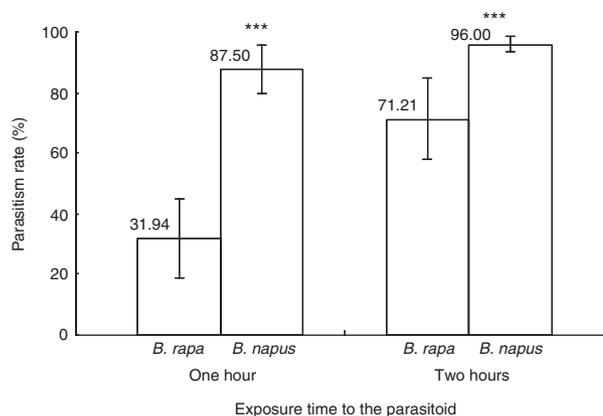

Fig. 1. Parasitism rate of Diamondback moth by *Cotesia plutellae* on *Brassica rapa* and *B. napus* (logistic analysis of deviance). *** represents a significance level of $P < 0.001$.
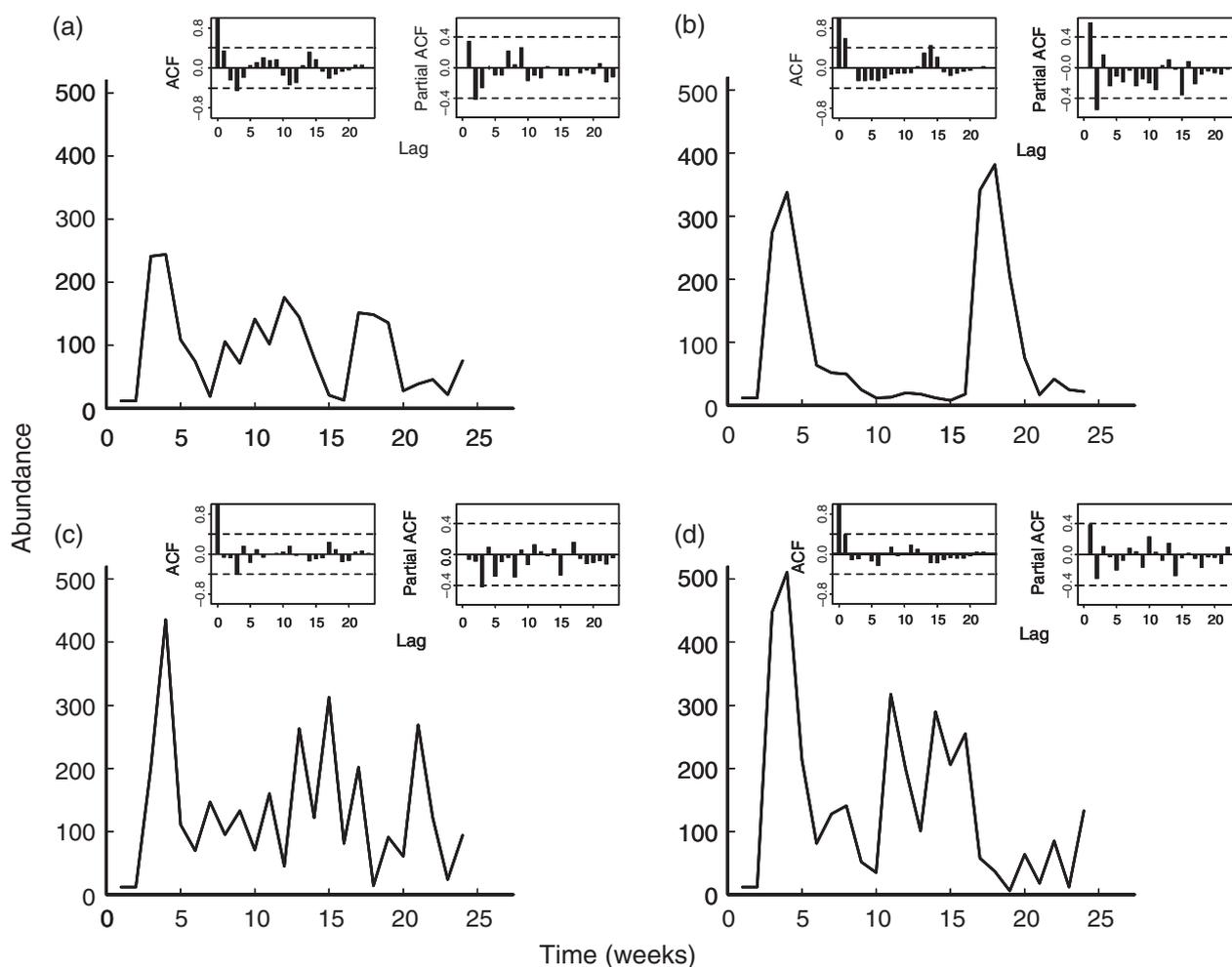
Fig. 2. Representative time series (of total live adults) for Diamondback moth populations on *Brassica rapa* (a, b), and Diamondback moth populations on *Brassica napus* (c, d).

for *P. xylostella* on *B. rapa* and *B. napus* showed no significant difference ($t_6 = 1.44$, $P = 0.2042$).

The time series also show no evidence for any regular fluctuations or cycles. Examination of the autocorrelation functions (Fig. 2) supported this idea that there were no periodic forcings or components in the population behaviour of *P. xylostella* on either of the two host-plant types. As the autocorrelation functions rapidly dampen out (Fig. 2) and the effect of long time lags have little influence on changes in current population size, these correlation

Table 1. Summary statistics of Diamondback moth populations on *Brassica rapa* and *B. napus* in absence of the parasitoid over the 24-week period of the experiment.

	Diamondback moth on *B. rapa*			Diamondback moth on *B. napus*		
Replicate	μ[a]	σ[b]	CV[c]	μ[a]	σ[b]	CV[c]
I	92.4	69.6	0.75	142.3	139.1	0.98
II	122.8	127.2	1.04	143.3	129.3	0.90
III	93.0	122.4	1.32	94.4	76.7	0.81
IV	121.0	140.3	1.16	131.2	105.1	0.80
Overall	107.3	117.0	1.09	127.8	115.0	0.90

[a]Mean number of live adults per cage per week.
[b]Standard deviation.
[c]Coefficient of variation (σ/μ).

statistics also indicate that the dynamics of *P. xylostella* are potentially driven by density-dependent processes.

To examine the variability in the population dynamics, comparisons within and between time-series treatments were made using coefficients of variation (as the variances were not constant and increased with the mean). Among time series of the same treatment, Diamondback moth populations feeding on *B. rapa* showed more variability [coefficient of variation (CV) between 0.75 and 1.32] compared to those on *B. napus* (CV from 0.80 to 0.98). Similarly, this result was consistent when overall variability between plant treatments was compared, indicating greater variability for Diamondback moth populations developing on *B. rapa* than on *B. napus* (1.09 vs. 0.90).

Density dependence analysis. The PACF correlograms showed differences between *P. xylostella* populations on the two host plants. For Diamondback moth populations on *B. rapa*, the PACFs exhibited significant correlations at lag one, two, or both, suggesting the dynamics are underpinned by a first- or second-order density dependent model. Whereas the PACFs for Diamondback moth on *B. napus* revealed that only one of the four replicates had a significant correlation at lag three.

To explore these descriptive patterns, autoregressive models of the net reproductive rate vs. lagged population densities were used. These models showed that the population dynamics of Diamondback moth on *B. rapa* were underpinned by delayed density dependence [$\ln(N_t) = 2.43 + 0.66 \ln(N_{t-1}) - 0.25 \ln(N_{t-2})$] (Fig. 3a). In contrast, direct density-dependent processes [$\ln(N_t) = 3.23 + 0.27 \ln(N_{t-1})$] determined the dynamics of Diamondback moth on *B. napus* (Fig. 3b).

Population dynamics: the effects of host-plant resistance on the population dynamics of Diamondback moth–C. plutellae

None of the replicates of the *P. xylostella–C. plutellae* interaction on the two host plants persisted for longer than 16 weeks (Fig. 4). In general, *C. plutellae* drove *P. xylostella* to extinction within five to nine generations after its introduction; however, in one population on *B. rapa*, Diamondback moth escaped extinction while *C. plutellae* was itself driven to extinction (Fig. 4b). Comparisons of the persistence time of the *P. xylostella–C. plutellae* interaction on the two different plants showed no significant difference ($t_6 = 0.3884$, $P = 0.7126$).

In the presence of *C. plutellae*, the mean number of Diamondback moth adults per week per cage on *B. rapa* varied between 74.3 and 111.4, and from 70.7 to 133.0 for Diamondback moth on *B. napus* (Table 2). However, comparison between the overall mean of *P. xylostella* population size on the different host-plant types showed no significant difference ($t_6 = 0.066$, $P = 0.95$). Furthermore, comparison between the overall means of the treatments with and without parasitoids on the same plant (Tables 1 and 2) did not show any significant difference (*P. xylostella* on *B. rapa*: $t_6 = 0.7634$, $P = 0.4742$; *P. xylostella* on *B. napus*: $t_6 = 1.542$, $P = 0.1768$). When overall variability was

compared, in the presence of *C. plutellae*, Diamondback moth populations feeding on the two host plants showed no difference (Table 2). However, as might be expected, the presence of the parasitoid increased the variability of Diamondback moth abundance on both host plants in comparison with the parasitoid-free treatments (Tables 1 and 2). In sum, in the presence of the parasitoid, *P. xylostella* populations on the two host plants revealed no difference in population size, variability, or persistence time.
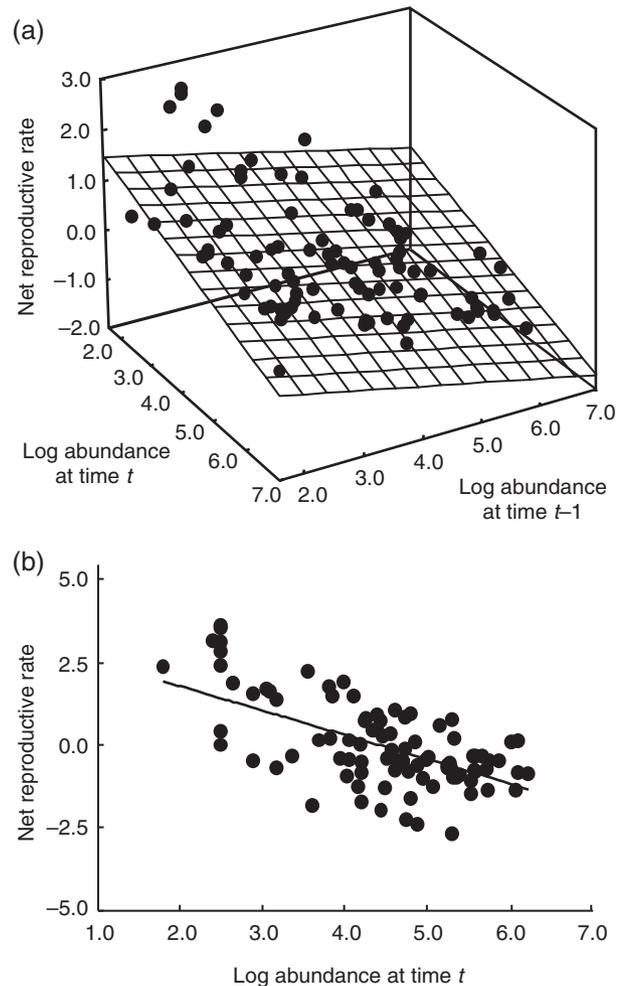
Fig. 3. Phase plots of net reproductive rate, $R_t = \ln(N_{t+1}/N_t)$, of Diamondback moth populations on *Brassica rapa* (a) and Diamondback moth populations on *Brassica napus* (b), plotted against natural log transformed population abundance (N_t and N_{t-1}). The best linear autoregressive models were a second-order model [$R_t = -0.2492$ (0.1003) $\ln(N_{t-1}) - 0.3415$ (0.1013) $\ln(N_t) + 2.4309$ (0.4072), $r^2 = 0.29$] for Diamondback moth populations on *B. rapa*, and a first-order model [$R_t = -0.73177$ (0.09813) $\ln(N_t) + 3.22687$ (0.44271), $r^2 = 0.37$] for Diamondback moth populations on *B. napus*. The numbers in parentheses represent the standard errors.
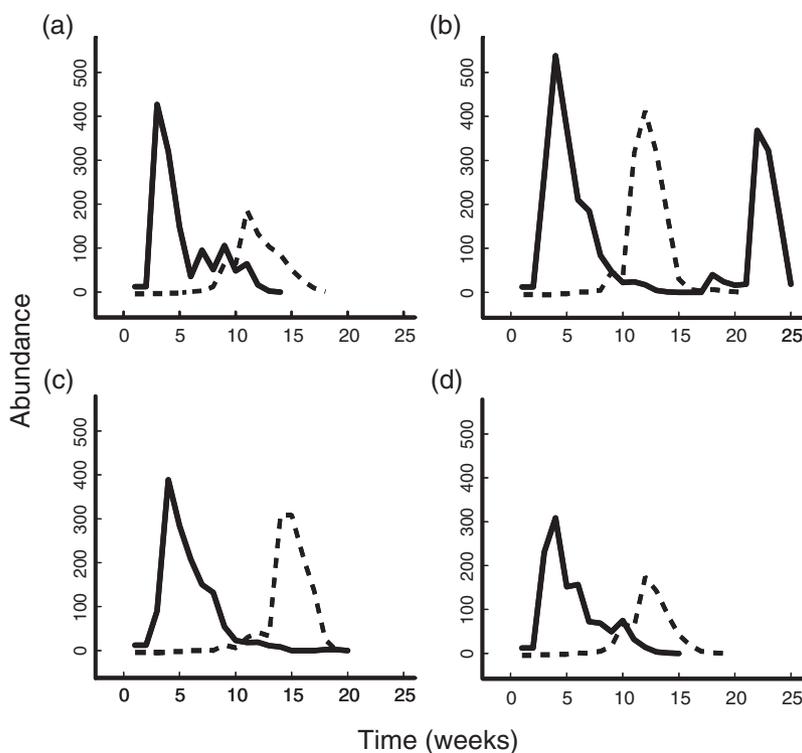
Fig. 4. Representative time series (of total live adults) for Diamondback moth and *Cotesia plutellae* populations on *Brassica rapa* (a, b), and Diamondback moth and *C. plutellae* populations on *Brassica napus* (c, d). Solid and dashed lines are Diamondback moth and *C. plutellae*, respectively.

Discussion

Here, using a series of replicated population dynamic and single cohort experiments it has been shown that differences in individual performance do not necessarily translate into differences in the population dynamics. Despite clear evidence of host plant-mediated effects on the short-term rates of parasitism (functional response) by *C. plutellae* on *P. xylostella*, underlying plant resistance or type had no effect on longer time scales and on the persistence time of the trophic interac-

tion between the moth and the parasitoid. In a similar way, even though host-plant resistance did not affect the equilibrial abundance of Diamondback moth, it clearly had a principal role in governing the different observed population dynamics.

Understanding this relationship between performance and dynamics is paramount in disentangling the effects of top-down and bottom-up effects. For instance, from a series of short-term experiments, Ramachandran *et al.* (1998) have shown that survival of Diamondback moth larvae on *B. rapa* was three times greater than that for Diamondback

Table 2. Summary statistics of Diamondback moth populations on *Brassica rapa* and *B. napus* in presence of the parasitoid over the period of the experiment.

	Diamondback moth on *B. rapa*			Diamondback moth on *B. napus*		
Replicate	μ^a	σ^b	CV^c	μ^a	σ^b	CV^c
I	95.4	127.2	1.33	70.7	109.5	1.55
II	111.0	151.8	1.37	113.7	130.0	1.14
III	111.4	136.9	1.23	79.2	93.4	1.18
IV	74.3	101.3	1.36	133.0	163.3	1.23
Overall	100.4	132.2	1.32	96.9	124.6	1.29

[a]Mean number of live adults per cage per week.
[b]Standard deviation.
[c]Coefficient of variation (σ/μ).

moth larvae on *B. napus* (50% vs. 17%). In comparison, the results of the work presented here show no difference in mean number of Diamondback moth on the two host plants at the population level. These contrasting results highlight that marked differences in individual performance do not necessarily translated directly into differences in the population dynamics. It has been well documented that feeding preference decisions by first-instar *P. xylostella* larvae is the principal mechanism of host-plant resistance (Eigenbrode & Shelton, 1990; Verkerk & Wright, 1996b; Eigenbrode & Pillai, 1998). Therefore, it is hypothesised that increased survival of Diamondback moth larvae on susceptible host plants will result in an increase in population size of competing larvae. In the absence of resource limitation this would lead to higher adult populations; however, the present study was run under resource-limited conditions in which high larval competition for food can result in reduced survival to adults. This clearly has implications for the population dynamics through the manifestation of density-dependent processes.

Here, the results from the time series showed that the dynamics of *P. xylostella* were principally influenced by density-dependent processes. Furthermore, the Diamondback moth populations on the two different host plants exhibited different dynamics due to different density-dependent effects. Diamondback moth populations on *B. napus* were affected by direct density-dependent processes and instantaneously responded to changes in their density [$N_{t+1} = f(N_t)$]. In contrast, the dynamics of Diamondback moth populations on *B. rapa* were determined by a delayed density-dependent process and there was a time lag in the response of Diamondback moth populations on *B. rapa* to its own density [$N_{t+1} = f(N_t, N_{t-1})$]. Intraspecific competition between moth larvae, which is likely to be more intense for moth populations feeding on *B. rapa* compared with those on *B. napus*, has a strong negative feedback on population growth rate, which can result in delayed density dependence. However, this negative feedback may not only be due to competition for food (limited resources) but also due to physical contact between individuals in high-density interactions (Møller, 1988).

As mentioned, delayed density dependence introduces time lags into the response of population change to population abundance. These effects can give rise to fluctuations in the herbivore populations leading to cycles or chaotic population dynamic behaviour. One of the principal ways that time lags can be generated and lead to oscillatory population dynamics is through maternal effects (Ginzburg & Taneyhill, 1994; Dwyer, 1995). Indeed, population quality can influence population size through maternal effects either directly in the current generation or in a delayed way in subsequent generations (Prout & McChesney, 1985; Rossiter, 1995). It is entirely plausible that host-plant quality can affect *P. xylostella* through such delayed, maternal effects (Behmer & Grebenok, 1998; Sayyed & Wright, 2001); this effect is likely to be sufficient to influence the population dynamics such that offspring performance

(survival and fecundity) is influenced by the bottom-up effects of the host plant and remains an area for future work.

The results presented here show that host-plant resistance can affect the rate of parasitism of *P. xylostella* by *C. plutellae*. However, in the long-term tritrophic population study, moth population size, variability, and the persistence time of the interaction were not influenced by host-plant type. These results again highlight that the results of individual performance may be totally different from those observed at the population level. Here, it has been shown that the lack of persistence of the interaction between *P. xylostella* and *C. plutellae* was principally due to the extinction of Diamondback moth (seven cases). The time to extinction was not determined by host-plant type (as host-only interactions persisted) but was due to the dynamical interaction between the insect herbivore and its parasitoid. The observed diverging oscillations between a host and its parasitoid are a consequence of overexploitation of the moth by *C. plutellae*, leading to the rapid extinction of the interaction (Nicholson & Bailey, 1935). Given that the host-only populations are regulated, the limited persistence of the *P. xylostella*–*C. plutellae* interaction suggests that the lack of available (temporal or spatial) refuges from a randomly foraging natural enemy is the principal mechanism that underpins the observed host–parasitoid dynamics.

In summary, it has been demonstrated that known individual performance on different host-plant types does not necessarily affect equilibrial population abundances but can affect the mechanisms by which populations are regulated. In tritrophic interactions, differences in host-plant type might be overwhelmed by the response of the natural enemy. Understanding the role of these bottom-up and top-down forces on the dynamics and persistence of *P. xylostella* remains a central focus for developing integrated control strategies for this pest species.

Acknowledgements

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