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Host plant nutritional quality affects the performance of the parasitoid *Diadegma insulare*

M. Sarfraz [a,*], L.M. Dosdall [b], B.A. Keddie [a]

[a] Department of Biological Sciences, University of Alberta, Edmonton, Alberta, Canada T6G 2E9
[b] Department of Agricultural, Food and Nutritional Science, University of Alberta, Edmonton, Alberta, Canada T6G 2P5

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ABSTRACT

The well documented biochemical profile of Brassicaceae, oligophagy of the herbivore *Plutella xylostella* (L.) (Lepidoptera: Plutellidae), and host specialization of the parasitoid *Diadegma insulare* (Cresson) (Hymenoptera: Ichneumonidae) provide an ideal system for investigating tritrophic interactions mediated by nutritional quality of plants. We evaluated the bottom-up effects of five soil fertility regimes on nutritional quality of canola (*Brassica napus* L.) and then on several fitness correlates of female and male *D. insulare* as mediated through *P. xylostella*. Variation in soil fertility influenced the nutritional quality of host plants and this in turn affected the performance of *D. insulare*. In general, *D. insulare* performed best on plants grown with 3.0 g fertilizer pot^{-1}; these plants had 2.06-, 3.77-, and 1.02-fold more nitrogen, phosphorous and potassium, respectively than ones grown without any added fertilizer. *P. xylostella* escape from *D. insulare* was highest (32%) on plants grown at 1.0 g fertilizer, and this could be attributed to both physical and physiological defense mechanisms mediated by host plant nutritional quality. Plant stress and plant vigor are competing paradigms pertaining to the performance of herbivorous insects on their host plants. These hypotheses were originally proposed to predict responses of herbivores, but may also explain the effects of plant quality on koinobiont parasitoids, such as *D. insulare*.

1. Introduction

In terrestrial systems where herbivory is common, bottom-up effects of plants may be of crucial importance (Price et al., 1980; Polis and Strong, 1996; Ode, 2006). The interactions between herbivorous insects and their host plants are undoubtedly influenced by host plant quality that can be determined largely by variation in certain abiotic (Hunter and Price, 1992; Moon et al., 2000) and biotic factors (Masters et al., 2001; Soler et al., 2007a,b; Sarfraz et al., in press). Perhaps one of the most important abiotic factors that shapes these interactions is nutrient availability and the subsequent nutrient contents of host plant tissues. Hypotheses of 'plant stress' and 'plant vigor' have been proposed to predict the response of insect herbivores to soil nutrients, as mediated by host plant quality. Some studies have shown that insects perform better on vigorous plants than on their stressed counterparts (e.g., Fox et al., 1990; Price, 1991; Meyer and Root, 1996; Craig and Ohgushi, 2002; Dosdall et al., 2004), while others indicate that stressed plants frequently support higher densities of insect herbivores (e.g., White, 1969; Mattson, 1980; Jones and Coleman, 1988).

The effects of soil nutrient regimes are relatively well studied for herbivores, but studies focusing on the effects of plant fertilization on parasitoids are rare. A parasitoid has to deal with a variety of challenges for its success, including host habitat identification, host location, host acceptance, host suitability and host regulation. Nutritional quality of host plants can be important at every step affecting parasitoid preference and performance indirectly or directly. Plants are known to indirectly influence the foraging efficiency of parasitoids, while plants directly influence host acceptance, host suitability and host regulation (Tumlinson et al., 1992; Poppy, 1997; Turlings and Benrey, 1998). A few experimental studies have indicated that abiotically induced changes in host plant quality can have strong effects on the performance of parasitoids. For example, *Anagrus armatus* (Ashmead) (Hymenoptera: Mymaridae) parasitized significantly more eggs of the salt marsh planthopper, *Pissonotus quadripustulatus* van Duzee (Homoptera: Delphacidae) on fertilized than on unfertilized plants (Moon et al., 2000). Plant nutritional quality can influence host-size and most host-size models assume that larger hosts are superior to smaller hosts in terms of parasitoid fitness. The evidence in support of such host-size models comes mainly from studies of non-feeding hosts (e.g., eggs and pupae) that contain a fixed quantity of resources for idiobiont parasitoids (Salt, 1940; Arthur and Wylie, 1959; Charnov et al., 1981; King, 1989; Corrigan and Lashomb, 1990; Moon et al., 2000; Moreau et al., 2009). In contrast to

* Corresponding author. Address: CW-405 Biological Sciences Centre, University of Alberta, Edmonton, Alberta, Canada T6G 2E9. Fax: +1 780 492 9234.
E-mail addresses: rsarfraz@ualberta.ca, sarfrazranapk@yahoo.com (M. Sarfraz).

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non-feeding hosts, insect herbivores continue to feed and develop after parasitization by koinobiont parasitoids until destructive consumption of their host (Jowyk and Smilowitz, 1978; Beckage and Riddiford, 1983; Sequeira and Mackauer, 1992; Harvey et al., 1995; Fox et al., 1996). Therefore, the quality of plant tissue consumed by herbivore hosts after parasitization may have stronger bottom-up influences on the performance of koinobionts than on idiobionts.

The diamondback moth, *Plutella xylostella* (L.) (Lepidoptera: Plutellidae), is a specialist on Brassicaceae (Talekar and Shelton, 1993; Idris and Grafius, 1996; Sarfraz et al., 2006), a family of plants characterized by the presence of sulfur-containing secondary plant compounds, the glucosinolates (Mithen, 1992). *Diadegma insulare* (Cresson) (Hymenoptera: Ichneumonidae) is a solitary koinobiont, host-specific larval endoparasitoid of *P. xylostella* and is one of its most important biological control agents in North America (Sarfraz et al., 2005b). It parasitizes all four larval instars of *P. xylostella*. It kills and emerges from the pre-pupal stage of its host and spins its own cocoon inside the loosely woven cocoon of its host (Harcourt, 1960). Like other parasitoid species of herbivores, *D. insulare* utilizes plant cues to locate its *P. xylostella* hosts (Tumlinson et al., 1992; Turlings and Benrey, 1998; Ohara et al., 2003). The unique biochemistry of Brassicaceae, the oligophagous habit of *P. xylostella*, and host specialization of *D. insulare* provide an excellent model to investigate tritrophic interactions based on the nutritional quality of plants, but to our knowledge studies focusing on such interactions are uncommon (Fox et al., 1990, 1996; Bentz et al., 1996).

In view of the extensive worldwide economic importance of *P. xylostella*, and the vast areas of the planet seeded annually to brassicaceous crops (e.g., approximately 5 million ha devoted to canola production in western Canada alone), the question arises of whether soil fertility levels can be manipulated for enhanced biological control of this herbivore with *D. insulare*. In this study, the effects of different soil fertility regimes were examined, viz. no added fertility, two levels of intermediate fertility and two levels of high fertility on *Brassica napus* L. (Brassicaceae), and on performance parameters of the parasitoid, *D. insulare*, developing within larvae of *P. xylostella* that were feeding upon leaf tissues of *B. napus*. Several fitness correlates directly related to parasitoid population dynamics (e.g., level of parasitism, survival, pre-imaginal developmental time, larval herbivory, pupal weight, adult body weight, longevity without food, forewing area, and hindwing area) were investigated on *P. xylostella* feeding on plants grown under five soil fertility regimes. A further objective of this study was to investigate how male and female *D. insulare* respond to bottom-up forces when its *P. xylostella* host larvae were reared on host plants grown under different soil fertility treatments.

2. Materials and methods

2.1. Insects and plants

Laboratory colonies of *P. xylostella* and *D. insulare* were maintained on potted *B. napus* cv. Q2 plants at 22 ± 0.5 °C with 16 h L:8 h D. Moths and wasps collected from commercial fields of *B. napus* in Alberta, Canada were added to the culture every summer to maintain genetic diversity.

Brassica napus plants were grown individually in 15.2-cm-diameter pots using sterile Metromix-220 (W.R. Grace & Co., Ajax, Ontario, Canada) as a potting medium. Treatment plants were grown under four soil fertility regimes viz. 0.5, 1.0, 3.0 and 5.0 g pot^{-1} of 20:20:20 (nitrogen:phosphorous:potassium) (Plant Products Co. Ltd., Brampton, Ontario, Canada), whereas control plants were grown without any added fertilizer. Fertilizer treatments were applied in two split applications to avoid any phytotoxic effects of higher concentrations: the first application was made after the second week of seed germination and the second application was made when plants were 3 weeks old. Each fertilizer treatment was applied after dissolving concentrate in 100 ml of tap water while control plants received 100 ml water only. Four-week-old plants were used for all experiments.

2.2. Intact plant study

2.2.1. Tissue nutrient analysis

Leaves from each replicate uninfested control plant were collected at the end of the larval development experiment (15–17 days, Section 2.2.2), air-dried at room temperature, ground and subjected to nutrient analysis. The combustion method (AOAC-990.03) was followed for determination of total nitrogen and sulfur (AOAC International, 2003a), whereas calcium, phosphorous, potassium, magnesium and sodium were assessed by using the inductively coupled plasma spectroscopic method (AOAC-985.01) in Norwest Labs, Lethbridge, Canada (AOAC International, 2003b).

2.2.2. D. insulare: parasitism, escape and survival

Over 500 newly emerged *P. xylostella* were allowed to oviposit on tinfoil sheets treated with an extract of *B. napus* leaves (Shelton et al., 1991). After 24 h, egg sheets were collected, excised in pieces each containing about 15–20 eggs, and incubated in individual plastic cups. Parasitism, escape and survival were assessed in screened cages (40 × 40 × 80 cm), arranged on greenhouse benches in a completely randomized design with each cage considered one replicate. Each cage contained a single plant; the entire experiment used 75 cages with 15 plants from each treatment. Ten plants from each treatment were infested with first-instar *P. xylostella* larvae from incubation cups at 10 larvae per plant by holding neonates carefully from their silk to avoid handling damage, while the remaining plants served as uninfested controls for tissue nutrient analysis (Section 2.2.1). Larvae were observed daily until they molted to second instars. Five plants of each soil fertility treatment received two female and two male wasps (⩽3 days old) whereas the remaining five plants of each soil fertility served as controls infested with *P. xylostella* only (see Sarfraz et al., 2005a); wasps were allowed to parasitize *P. xylostella* larvae for 24 h and were then removed from the cages. Larvae were kept on the same plants to complete development and observed every 48 h; the numbers of surviving larvae were recorded, but daily observations were made when pupation began. Pupae were harvested, weighed within 24 h of pupation and kept individually in labeled transparent plastic cups in a growth chamber at 22 ± 0.5 °C with 16 h L:8 h D until adult emergence. The numbers of individuals that successfully developed into *P. xylostella* pupae despite being exposed to *D. insulare* were considered to have escaped parasitism.

It was assumed that mortality of *P. xylostella* larvae other than control mortality was caused by parasitoids and the percent parasitism was calculated using the following equation:

$$\text{Parasitism}\ (\%) = [(P_{di} \div L_t) \times 100] + M_c$$

where P_{di} is the numbers of *D. insulare* pupae that developed, L_t the total numbers of *P. xylostella* larvae introduced to each cage, and M_c the percent corrected mortality determined by Schneider-Orelli's formula (Schneider-Orelli, 1947).

2.3. Leaf tissue study: pre-imaginal and imaginal parameters

This study was conducted in controlled environmental conditions in a growth chamber (22 ± 0.5 °C with 16 h L:8 h D). Excised leaves taken from uninfested plants were placed on moist filter papers (9-cm-diameter) in plastic containers covered with