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Influences of plant species on life history traits of *Cotesia rubecula* (Hymenoptera: Braconidae) and its host *Pieris rapae* (Lepidotera: Pieridae)

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ABSTRACT

The relative suitability of four plants was studied for larvae of *Pieris rapae* L. and its parasitoid *Cotesia rubecula* (Marshall). For unparasitized *P. rapae,* pupal dry weight and egg-pupa growth rate were higher on cabbage, radish and nasturtium than on Indian hedge mustard. Larval developmental rate and size were greatest for *C. rubecula* when its host was feeding on nasturtium. Wasp survival was not affected by the host insect/plant combination in which the parasitoid developed. These results indicate that the plant on which host larvae feed is an important factor in development of the parasitoid.

1. Introduction

The successful development of a parasitoid requires that its minimal nutritional requirements be satisfied by the resources available in its hosts. Therefore, host nutrition can have profound effects on the ability of a parasitoid to develop optimally (Hawkins, 1994; Brown, 1984; Abrahamson and Weis, 1997). Since many parasitoids attack hosts that can feed on several plant species (e.g., Greenblatt and Barbosa, 1981; Barbosa et al., 1982; Price, 1986), and since larval performance undoubtedly is a major component of parasitoid fitness, it is of theoretical and practical interest to determine whether host plants that promote rapid herbivore growth also promote rapid growth of larval parasitoids.

Parasitoid host relations can be influenced by the food plants of their respective hosts in two ways. Plants may affect the host selection activities of parasitoids (Mueller, 1983) or the nutritional quality of the host's food can influence parasitoid growth and survival (House and Barlow, 1961; DeMoras and Escher, 1990; Stamp, 2001). Several studies (Shapiro, 1956; Smith, 1957; Cheng, 1970; Greenblatt and Barbosa, 1981; Karowe and Schoonhoven, 1992) indicate that changes in the food-plant may change the host's value for parasitoids, but few attempts have been made to measure and compare host quality in relation to the plant on which it feeds (House, 1977; Karowe and Schoonhoven, 1992).

This study was designed to determine the relationship between the suitability of four plants for the cabbage white butterfly, *Pieris rapae* L. (Lepidoptera: Pieridae), and its parasitoid *Cotesia rubecula* (Marshall) (Hymenoptera: Braconidae). The aims of this study were to test the suitability of plant species for *P. rapae* and its parasitoid *C. rubecula*. In first part, the life history traits (larval developmental time, pupal dry weight, egg-pupa growth rate, pupa proportional dry weight, adult dry weight and egg-adult growth rate) of *P. rapae* were measured. In second part, I examined the suitability of *P. rapae* larvae reared on different plant species by measuring the life history traits (developmental time, adult wet weight, egg-adult growth rate and size) of *C. rubecula*. I argue the hierarchy of plant species suitability for *P. rapae* and its parasitoid *C. rubecula*.

2. Materials and methods

P. rapae was collected in Adelaide, South Australia and the culture was reared on potted cabbage (*Brassica oleracea* L. cv. Green Coronet) at 25 °C, 16L: 8D. Second instar larvae were used as hosts in the experiment involving parasitism. The wasp, *C. rubecula* was collected in Adelaide and the culture was reared on larvae of *P. rapae* on potted cabbage at 25 °C, 16L: 8D. Wasp cocoons were isolated in 18 mm diam. × 68 mm glass vials with a drop of honey. Upon emergence, females were caged serially, 2–4 at a time, with 10 males until each mated. Females were re-isolated in vials and held until used in experiments. Larval *P. rapae* were fed from hatching on radish (*Raphanus vulgaris* L.), Indian hedge mustard (*Sisymbrium orientale* L.), nasturtium (*Tropaelum majus* L.) and cabbage. All plants were 24–30 days old when used, and were grown from seed in a greenhouse.

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2.1. The influence of plant species on performance of P. rapae

To determine whether performance of *P. rapae* differs among the four plants two separate experiments were conducted; one focused on pupae and the other on adults of *P. rapae*. In the first experiment twenty five mature eggs were placed on three pots of each host plant at 25 °C under a photoperiod of 16L: 8D. Surviving individuals were weighed to 1 μg precision on a Beckman L-M-600 microbalance within 24 h of pupation and were frozen immediately after weighing, dried for 1 day at 60 °C and re-weighed to provide a dry weight/wet weight ratio (proportional dry weight). The second experiment was the same as the first except insects developed to the adult stage. Adults were sexed, frozen within 4 h of enclosing and dried for one day at 60 °C. Several measures of performance were calculated for *P. rapae* on each host plant: survivorship, egg-pupa and egg-adult growth rates (mg dry weight/developmental time in days), pupal and adult weights, larval and pupal developmental time and proportional dry weight.

2.2. The influence of plant species on performance of C. rubecula

To assess the effect of different host plants on performance of this parasitoid, *P. rapae* larvae were reared on the four different plant species separately in identical fashion to unparasitized larvae. Twenty five second instar larvae, 2–3 days of old at 25 °C (larval instar was determined by measuring the width of the head capsule, M.A. Keller unpublished data) from each host plant were placed in a 150 mm glass Petri dish with four mated female wasps and observed until the act of oviposition observed for all of them. Wasps were 2 days old and had mated 1 day before exposure to hosts. The parasitized larvae were transferred to plants and reared until they reached the pupal stage. The wasp *C. rubecula* exits from the last abdominal segment from exit hole and begins to spin cocoons formed of a very strong threaded silk after 24 h after egression from the host. Wasp's cocoons were isolated in 18 mm × 68 mm glass vials and were maintained at 25 °C until adult emergence, at which time the sex of each adult was determined. The length of the parasitoid's hind tibia as indication of body size was measured. Hind tibia is an index of exoskeleton size and is widely used in life history studies (Bai et al., 1992; Hohmann et al., 1988; Waage and Ng; 1984; Kazmer, 2008). Larval survivorship, larval developmental time, adult weight, eggs-adult growth rate (mg wet weight/developmental time in days) were recorded for each herbivore–host plant combination. The experiment was repeated twice.

Statistical analyses of results were carried out using factorial regression for unequal sample sizes among species, sexes and replicates (Neter and Wasserman, 1974). In this analysis, sex effect and interaction effect for sex and species were tested then pooled to compare the survivorship to pupa and adult of *P. rapae* and the survivorship to adult of *C. rubecula* among species. The survivorship to pupa and adult of *P. rapae* on plant species were examined using a Binomial error distribution. The numbers of parasitoids that emerged from the larvae that were fed on plant species were examined using a Poisson error distribution (Genstat, 1987). Differences between means were examined by Scheffe's test (Groebner and Shannon, 1990).

3. Results

3.1. Influence of plant species on performance of P. rapae

Larval developmental time, pupal dry weight, egg-pupa growth rate, pupa proportional dry weight, adult dry weight and egg-adult growth rate were all affected by plant species (Table 1). Development time ($F = 21$, df = 3, 55, $P < 0.001$) was shorter on cabbage and nasturtium and longer on radish and Indian hedge mustard. There were no differences between sexes. Pupal dry weight ($F = 21$, df = 3, 55, $P < 0.001$) was lowest on Indian hedge mustard than other species (Table 1) and differed between sexes. Males and females followed the same pattern. Egg-pupa growth rate ($F = 7$, df = 3, 55, $P < 0.001$) was higher on cabbage, nasturtium and radish than on Indian hedge mustard in both male and female (Table 1). Proportional dry weight ($F = 7$, df = 3, 55, $P < 0.001$) of *P. rapae* in pupa was lowest on Indian hedge mustard and there were no differences between sexes (Table 2). Variation in adult dry weight ($F = 11$, df = 3, 63, $P < 0.001$) and egg-adult growth rate ($F = 22$, df = 3, 63, $P < 0.001$) were similar to pupae. Patterns observed in survival of *P. rape* (pupa and adult) was not affected by plant species ($\chi^2 = 1.2$, df = 3, $P > 0.7$).

3.2. Influence of plant species on performance of C. rubecula

Overall survival of *C. rubecula* within caterpillars that survived until parasitoid egression was 69% and was not affected by host plant species ($\chi^2 = 0.8$, df = 3, $P > 0.9$) (Table 3). A large number of *P. rapae* that had been parasitized by *C. rubecula* died, presumably due to mutilation of the host at the time of oviposition. Adult developmental time ($F = 8.4$, df = 3, 129, $P < 0.001$), weight ($F = 3.92$, df = 3, 129, $P < 0.025$), size ($F = 2.76$, df = 3, 129, $P < 0.05$) and egg-adult growth rate ($F = 6.71$, df = 3, 129, $P < 0.001$) were affected by the sex and by the host plant species. The development time of female wasps emerged from hosts fed on nasturtium were shorter (15.0 ± 0.1) than those wasps emerged from hosts fed on Indian hedge mustard (16.1 ± 0.2), radish (15.8 ± 0.1), and cabbage (15.5 ± 0.1). The development time of male wasps followed the same pattern as female wasps.

Table 1
Performance of *P. rapae* pupa on cabbage (CA), nasturtium (NA), radish (RA) and Indian hedge mustard (IHM). Means are given with standard errors. Means within columns followed by different letters are significantly different by Scheffe's test ($P = 0.05$). Developmental times are in days, weights are in mg, growth rates are in mg dry wt/day, and proportional dry weight was calculated by mg dry weight/wet weight.

Host plant	*N*		Larval development time	Pupal dry weight		Egg-pupa growth rate	
	Male	Female		Male	Female	Male	Female
CA	8	9	16.0 ± 0.05a	3.7 b ± 0.07b	4.1 ± 0.07b	0.23 ± 0.003b	0.26 ± 0.004b
NA	4	6	17.0 ± 0.00a	3.4 ± 0.16b	4.1 ± 0.13b	0.20 ± 0.01b	0.24 ± 0.009b
RA	10	11	18.5 ± 0.33 b	3.6 ± 0.10b	4.1 ± 0.09b	0.20 ± 0.006b	0.23 ± 0.004b
IHM	7	8	18.2 ± 0.26b	3.1 ± 0.09a	3.31 ± 0.11a	0.17 ± 0.007a	0.18 ± 0.005a
	N		*Proportional dry weight*				
CA	17		0.23 ± 0.002b				
NA	10		0.22 ± 0.003b				
RA	21		0.23 ± 0.002b				
IHM	15		0.20 ± 0.007a				

Table 2
Performance of *P. rapae* adult on cabbage (CA), nasturtium (NA), radish (RA) and Indian hedge mustard (IHM). Differences in survivorship were determined by using a Binomial error distribution test. Means are given with standard errors. Means within columns followed by different letters are significantly different by Scheffe's test ($P = 0.05$). Weights are in mg and growth rates are in mg dry wt/day.

Host plant	*N*		Larval survivorship*	Adult dry weight		Egg-adult growth rate	
	Male	Female		Male	Female	Male	Female
CA	9	11	20	2.5 ± 0.08b	2.7 ± 0.06b	0.13 ± 0.003b	0.13 ± 0.003b
NA	8	6	14	2.4 ± 0.08b	2.8 ± 0.06b	0.12 ± 0.003b	0.14 ± 0.004b
RA	8	11	19	2.5 ± 0.09b	2.9 ± 0.07b	0.12 ± 0.003b	0.14 ± 0.006b
IHM	10	8	18	2.2 ± 0.05a	2.3 ± 0.08a	0.10 ± 0.003a	0.10 ± 0.003a

* Larval survivorship across all host plants $\chi^2 = 1.2$, df = 3, $P > 0.7$.

Males are lighter and smaller than females. The female wasp *C. rubecula* emerging from hosts fed on nasturtium (2.1 ± 0.06), and cabbage (2.1 ± 0.08) had higher wet weights than those on Indian hedge mustard (1.8 ± 0.15) and radish (1.8 ± 0.1). The male wasps emerging from hosts fed on nasturtium (1.7 ± 0.07), cabbage (1.7 ± 0.1) and radish (1.5 ± 0.1) showed lower wet weights compared to those wasps on Indian hedge mustard (1.8 ± 0.07).

The female wasps that emerged from hosts fed on nasturtium (1.2 ± 0.02) were larger than those wasps on Indian hedge mustard (1.1 ± 0.01), cabbage (1.1 ± 0.01) and radish (1.1 ± 0.01) as measured by lengths of hind tibia. The male wasps emerged from hosts fed on cabbage were smaller (1.0 ± 0.01) than those on other host plant species (1.1 ± 0.02).

Egg-adult growth rate was significantly greater for the female wasps fed on nasturtium (0.15 ± 0.01) and cabbage (0.14 ± 0.01) than on any the other host plant species (Table 3). The male wasps reared from cabbage-fed host larvae had lower egg-adult-growth rate (1.0 ± 0.01) than on other host plant species (Table 3).

4. Discussion

Four host plant species were compared with regard to relative suitability as a food source for *P. rapae* and its parasitoid *C. rubecula*. The results indicate that the diet of host is an important factor in the suitability of hosts for this parasitoid.

Karowe and Schoonhoven (1992) studied the relative suitability of four different host plants for *Cotesia glomerata* developing in *Pieris brassicae*. For *P. brassicae* growth rate and pupal weight were highest on Brussels sprouts and Swedish turnip, intermediate on rape, and lowest on nasturtium. Nasturtium was the most suitable host for *C. glomerata* developing in *P. brassicae* (Karowe and Schoonhoven, 1992). Larval developmental rate and adult longevity were greatest for *C. glomerata* from *P. brassicae* reared on nasturtium (Karowe and Schoonhoven, 1992). Similar responses to nasturtium observed in *C. glomerata* and *C. rubecula* could indicate a similar relationship between these two parasitoids.

For *P. rapae*, plants compared to Indian hedge mustard are more suitable as seen by larval development time, pupa dry weight, egg-pupa growth rate, pupa proportional dry weight, egg-adult growth rate and adult dry weight. In turn, nasturtium is the most suitable plant for *C. rubecula* in terms of the shortest development time, highest weight, highest egg-adult growth rate and largest size. The positive relationship between shorter developmental time and larger body size is associated with fitness (Doyon and Boivin, 2005). This indicates that environmental effects that favoured short developmental time were also favoured for larger body size (Waage and Ng, 1984). Cabbage was in the same rank of suitability with nasturtium in terms of development time, weight and egg-adult growth rate. Indian hedge mustard was in the same rank of suitability with radish in terms of development time, weight, size and egg-adult growth rate.

There might be a positive correlation between host plant suitability for hosts and for their parasitoids, for instance, vigorous hosts feed more and therefore produce more body tissue and/or hemolymph on which the parasitoid can feed (Karowe and Schoonhoven, 1992; Mueller, 1983). In these cases nasturtium and cabbage seem to be more nutritious plants for *P. rapae* and *C. rubecula* as they promote the growth of host and parasitoid.

Wasp size is affected by the plant species on which its host caterpillar feeds (Price, 1986; Guillot and Vinson, 1973; Zohdy and Zohdy, 1976; Beckage and Riddiford, 1983; Liu, 1985; Mackauer, 1986; Slansky, 1986), where development of the wasps is synchronized with the host, plant species may change host suitability and parasitoid development time (Pierce and Holloway, 1912). There is a correlation between length of hind tibia and number of eggs and oocytes present in female *C. rubecula* (Talaei, unpublished, ($r = 0.45$, $n = 72$, $P < 0.001$), suggesting that, as in many other insects, larger females possess a fecundity advantage over smaller females (Waage and Ng, 1984; Bellows, 1985; Van den Assem et al.,

Table 3
Performance of *C. rubecula* developing in *P. rapae* feeding on cabbage (CA), nasturtium (NA), radish (RA) and Indian hedge mustard (IHM). Values are means ± standard errors. Means within columns followed by different letters are significantly different by Sheffe's test ($P = 0.05$). Development time's are in days, weights are in mg and growth rates are in mg wt/day. Size's are in mm. Differences in survivorship were determined by a Poisson error distribution test.

Host plant	*N* (Larval survivorship) *		Developmental time (Egg to adult)		Adult weight	
	Female	Male	Female	Male	Female	Male
CA	13	19	15.5 ± 0.1b	15.3 ± 0.3b	2.1 ± 0.08b	1.7 ± 0.1a
NA	18	21	15.0 ± 0.1a	14.2 ± 0.1a	2.1 ± 0.06b	1.7 ± 0.07a
RA	12	21	15.8 ± 0.1b	15 ± 0.2b	1.8 ± 0.1a	1.5 ± 0.1a
IHM	22	12	16.1 ± 0.2b	15.4 ± 0.1b	1.8 ± 0.1a	1.8 ± 0.07b
	N		*Egg-adult growth rate*		*Egg-adult growth rate*	
CA	13	19	1.1 ± 0.01a	1.0 ± 0.01a	0.14 ± 0.01b	1.0 ± 0.01a
NA	18	21	1.2 ± 0.01b	1.1 ± 0.02b	0.15 ± 0.01b	1.1 ± 0.02b
RA	12	21	1.1 ± 0.01a	1.1 ± 0.01b	0.12 ± 0.01a	1.1 ± 0.01b
IHM	22	12	1.1 ± 0.01a	1.1 ± 0.00b	0.12 ± 0.01a	1.1 ± 0.00b

* Larval survivorship across host plant species $\chi^2 = 0.8$, df = 3, $P > 0.9$.

1989). In this study, host suitability, as measured by adult size, and developmental rate for an individual parasitoid is influenced by the host's food, such that in the case *C. rubecula*, larger and potentially more vigorous individuals emerged from hosts reared on certain host plants (Godfray, 1994; Price et al., 1980; Awmack and Leather, 2002).

Fecundity is correlated with size, population dynamics are expected to vary with the host's diet (Baltensweiler et al., 1976; Mattson and Addy, 1975; Gilbert, 1976; Edmunds and Alstad, 1978; Barbosa, 1978; James and Partridge, 1998; Van Nouhuys and Hanski, 1999). This could indicate that the regulatory impact of parasitoids on herbivore populations could be influenced by the herbivore–host plant relationship (Mueller, 1983). I have shown that intra-specific variability of hosts caused by feeding on different food plants may influence host suitability for parasitoid. This could have a significant influence on the success of biological control of polyphagous herbivores (Greenblatt and Barbosa, 1981). The results of this study showed that the plants can influence parasitoid–host relationships (Price et al., 1980; Cronin and Abrahamson, 2001; Lill et al., 2002) and in studies of host/parasitoid interactions must consider the role of plants.

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