



## Host plant selection and development in *Spodoptera exigua*: do mother and offspring know best?

Mariano Berdegué<sup>1</sup>, Stuart R. Reitz\* & John T. Trumble

Department of Entomology, University of California, Riverside, CA 92521–0314 USA; \*Author for correspondence; <sup>1</sup>Present address: Monsanto Comerial SA de CV, Mexico City, DF11700, Mexico

Accepted August 18, 1998

**Key words:** host preference, insect-plant interactions, behavior, oviposition

### Abstract

We examined the ovipositional preference and larval development of *Spodoptera exigua* (Hübner) (Lepidoptera: Noctuidae) on two common hosts in southern California, *Chenopodium murale* L. (Chenopodiaceae) and *Apium graveolens* L. (Umbelliferae) to determine if female oviposition preference is correlated with offspring performance. Greenhouse oviposition choice tests indicated that *S. exigua* oviposit more frequently on *C. murale* than on *A. graveolens*. However under laboratory conditions, larvae reared on *C. murale* had longer development times, lower relative growth rate, and lower survivorship than larvae reared on *A. graveolens*. larval and pupal masses were significantly greater on *A. graveolens* than on *C. murale*. Furthermore, pupal masses were significantly greater for individuals reared on *A. graveolens* than on *C. murale*. Because pupal masses and adult fecundity are positively correlated for *Spodoptera* spp., the fitness of *S. exigua* on *A. graveolens* is likely to be substantially higher than its fitness on *C. murale*. Despite better larval performance on *A. graveolens*, previous results from choice tests with whole plants and leaf discs indicate that the highly mobile *S. exigua* larvae strongly prefer *C. murale* over *A. graveolens*. Hypotheses attempting to explain this lack of correlation between larval and adult host preference versus development and survival in this system are discussed.

### Introduction

In Lepidoptera, host plant selection for larvae is commonly assumed to be the prerogative of the ovipositing female (Singer, 1984). Using this assumption, many studies have investigated the relationship between adult host preference and offspring performance (Remington, 1952; Straatman, 1962; Wiklund, 1975; Courtney, 1981, 1982; Rausher, 1982; Rausher & Papaj, 1983; Thompson, 1983; Singer, 1984; Legg et al., 1986; Karban & Courtney, 1987; Damman & Feeney, 1988; Auerbach & Simberloff, 1989; Fox & Eisenbach, 1992; Nylin & Janz, 1993; Singer et al., 1994). Although one would intuitively expect a positive correlation between adult host preference and offspring performance, such a relationship does not always exist (Remington, 1952; Straatman, 1962; Wiklund, 1975; Chew, 1977; Rodman & Chew, 1980; Courtney, 1981, 1982; Singer, 1984; Legg et al., 1986; Karban &

Courtney, 1987; Auerbach & Simberloff, 1989; Fox & Eisenbach, 1992; Singer et al., 1994). The absence of a positive correlation between adult oviposition preference and offspring development has been explained, in part, because the relationship between host choice and larval performance varies under different ecological conditions and selection pressures (Thompson, 1988).

In addition, many species of Lepidoptera have highly mobile larvae that can engage in host plant selection (Chew, 1977; White & Singer, 1974; Wiklund, 1975, 1984; Smits et al., 1987; Carriere, 1992; Bernays & Chapman, 1994; Berdegué & Trumble, 1996). If nutritional benefits are a major force either driving or reinforcing host plant preference (Scriber & Slansky, 1981; Bernays & Chapman, 1994), one would expect the insect herbivore (especially the larvae) to choose the 'best' food source (i.e., host plant) for development. Yet again, other selection pressures can impact host plant preference of mobile herbivores.

To our knowledge, there are few data relating host selection by both larvae and adults with larval performance of lepidopteran insects (but see Nylin & Janz, 1996).

*Spodoptera exigua* (Hübner) (Lepidoptera, Noctuidae) has highly mobile larval and adult stages, and is known to feed on more than 50 plant species from over ten families around the world (Wilson, 1932; Smits et al., 1987). This species apparently originated in southern Asia, and was introduced into the USA in Oregon in 1876 and again in California in 1882 (Wilson, 1932). Since its introduction to California, *S. exigua* has become an important pest of celery, *Apium graveolens* L. (Umbelliferae) (Van Steenwyk & Toscano, 1981; Diawara et al., 1996). However, *A. graveolens* is not necessarily a preferred host. Recent studies have demonstrated that the larvae prefer the common weed *Chenopodium murale* L. (Chenopodiaceae) over *A. graveolens* (Berdegué & Trumble, 1996). Our objectives for this study were to determine if oviposition preference and the previously observed larval preference are correlated with larval performance of *S. exigua* on *A. graveolens* and *C. murale*. Hence, we tested the working hypotheses that females of *S. exigua* oviposit preferentially on a host that is preferred by larvae (i.e., *C. murale*), and that a superior host plant in terms of its nutritional value for *S. exigua* development is one on which larvae feed preferentially (i.e., *C. murale*).

## Materials and methods

All insects were obtained from an *S. exigua* colony maintained at the University of California, Riverside (UCR). The colony, originally collected from Orange County, CA in 1982, has been maintained on artificial diet modified from Patana (1969), in incubators at  $28 \pm 2^\circ\text{C}$  and L14:D10. New genetic material from the same geographic area has been incorporated into the colony annually since 1983, with the most recent addition being two months prior to the study. Additions to the colony were made by collecting larvae and rearing them in isolation to screen for parasites and pathogens. Adults from these field-collected larvae were crossed, and the F1 progeny of those adults were incorporated into the colony.

**Oviposition preference.** Test plants were held in a greenhouse ( $25 \pm 4^\circ\text{C}$  and 50% r.h.) at UCR. We transplanted *A. graveolens* (var. 'Conquistador') seedlings

into 10 cm<sup>2</sup> plastic pots, three months prior to the study. *C. murale* seedlings were transplanted into plastic pots, from a field in the UCR Agricultural Experiment Station (Riverside, CA), four months prior to the study.

The oviposition preference tests were conducted inside three octagonal cages (1 m in diameter  $\times$  1 m high) constructed using PVC pipes (2.0 cm in diameter). Spun-bonded polyester floating row cover (Remay, Dupont Co., Wilmington, DE) was clipped to the top and sides of the cage; the bottom was left open.

We placed two (each) *A. graveolens* and *C. murale* plants of similar size in a soil-filled greenhouse bench (1.5 m wide  $\times$  15 cm deep). Plants of the same species were placed in opposite corners of a square design (45  $\times$  45 cm). These positions were randomly assigned for each replicate. The pots were buried in the soil such that they were completely hidden. Cages were placed over the plants. There were three cages per replicate (each cage with two *C. murale* and two *A. graveolens* plants); the entire experiment was repeated three times.

*Spodoptera exigua* pupae were sexed and placed inside cylindrical cardboard containers (3.78 l) with a vial containing 10% honey water solution as a source of nutrition. After emergence (12–18 h), two females, two males, and two honey water vials were placed in each of three new containers. The insects were left in these containers for five hours to allow for mating. At the end of this time period, we released two males and two females from each container inside each oviposition arena. Two vials containing honey water were provided in each cage.

Each replicate had a five day duration after which the adults were captured. The plants were dissected and the number and position (upper, middle, and bottom third of the plant) of egg-clusters per plant, and the number of eggs per egg-cluster were recorded. We excised the plant part containing each egg-cluster and placed it inside a cup (192 ml) with artificial diet. These cups were placed in an incubator at  $28 \pm 2^\circ\text{C}$  and L14:D10. Subsequently, the numbers of emerging neonates were recorded as a measure of plant effect on egg fitness.

The number of egg-clusters per cage, number of eggs per cage, and number of neonates per cage were calculated by adding the number of egg-clusters per plant, number of eggs per plant, and number of neonates per plant for the two plants of the same species within a cage. Preference within each of the

recorded variables was calculated by subtracting the numbers on *A. graveolens* from the numbers on *C. murale* (i.e., a negative value for number of eggs indicates more eggs on *A. graveolens*). The few egg-clusters found directly on the cage (average < 1/cage) were not included in the analyses.

**Developmental test.** *Chenopodium murale* was sown into a field at the UCR Agricultural Experiment Station on April 1, 1995. On April 13, we transplanted *A. graveolens* (var. 'Conquistador') plants (40 days after germination) into a row in the same field. The typical pattern of weed infestation was created; *C. murale* was largely limited to furrows while *A. graveolens* developed on beds. Standard commercial cultural and irrigation practices were followed (see Koike et al., 1996).

We conducted developmental studies in the laboratory using leaf material from both plant species. One unfed neonate (0–12 h old) was placed inside a 30 ml plastic cup with 4% agar in the bottom (after Diawara et al., 1992) and with one leaf of either *C. murale* or *A. graveolens*. Although these insects will eat nearly any above-ground plant structure, leaves were chosen as the experimental unit because *S. exigua* larvae are most commonly observed feeding on leaves (Griswold & Trumble, 1985). The leaves were randomly collected from the plants and were replaced every other day or when 50% of the leaf material had been consumed, whichever came first. Initially only one fully-expanded leaf was added to each cup. This increased to three leaves for late third stadium through prepupal larvae.

The larvae were individually weighed to the nearest 0.001 mg at 3, 4, 5, 6, 7, and 9 d. In addition pupae were weighed one day after pupation. We also recorded days to pupation, days to adult emergence (days from pupation to adult eclosion), and survivorship. The relative growth rate (mg/mg larva/day) was estimated as ([mass day 9-mass day 3]/average mass over the 6 days)/6 days (Eigenbrode et al., 1993).

There were 22 replications (22 individual larvae) per plant species and the experiment was repeated four times. The first repetition was conducted 81 days (July 3, 1995), the second 89 (July 11, 1995), the third 95 days (July 17, 1995), and the fourth 99 days (July 21, 1995) after *A. graveolens* was transplanted. These tests were conducted under the same environmental conditions as used for colony maintenance. Larvae for each replicate hatched from eggs laid the same night in the main laboratory colony.

**Statistical analyses.** Prior to analysis, oviposition data were transformed using the formula  $y = \log(x + 100)$ , where  $x$  is the number of eggs, egg clusters, or neonates per cage. Then the assumption of normality was tested for all data, using the UNIVARIATE procedure (SAS, 1990). We used analysis of variance to determine if there were significant differences among cages or replicates for the oviposition preference tests. We then performed paired *t*-tests on untransformed variables to test for differences between *C. murale* and *A. graveolens*.

To test for possible positional preferences in oviposition (e.g., greater number of eggs laid on the bottom third of either plant species) we included a third main effect in the model (position). The error term for cage nested within repetition (repetition [cage]) was used to test for a repetition effect (e.g., possible phenological differences).

The assumption of normality was tested for all development data, using the UNIVARIATE procedure of the Statistical Analysis System (SAS, 1990). Proportion survival data were transformed with the arcsine of the square root prior to examination for normality. Normally-distributed developmental data were analyzed using an analysis of variance (ANOVA) with repetition and treatment (plant species) as main effects. Non-normally distributed data were analyzed with via nonparametric analysis of variance test (Friedman's method for randomized blocks, Sokal & Rohlf, 1995).

## Results

**Oviposition preference.** Cage and repetition effects were non-significant ( $P > 0.30$ ) for all of the oviposition tests and will not be considered further. *S. exigua* adults laid significantly more egg-clusters and eggs on *C. murale* than on *A. graveolens* (Table 1). As a result of the difference in number of eggs laid on the plants, numbers of emerging neonates were also significantly greater on *C. murale*. However, the proportion of eggs successfully hatching was not significantly greater on *C. murale*. There were no preferences for plant position by ovipositing females for either plant species. The number of egg-clusters per cage, number of eggs per cage, and number of emerging neonates per cage between the upper, middle, and bottom third were not significantly different for either *C. murale* (egg-clusters:  $F = 2.41$ ,  $df = 2$ ,  $P = 0.13$ ; eggs:  $F = 1.57$ ,  $df = 2$ ,  $P = 0.25$ ; neonates:  $F = 0.37$ ,  $df = 2$ ,  $P = 0.70$ ) or

Table 1. Results of *S. exigua* ovipositional preference tests between *C. murale* and *A. graveolens*

	<i>C. murale</i> (mean $\pm$ SE)	<i>A. graveolens</i> (mean $\pm$ SE)	t value	df	P value (1 tailed)
Egg-clusters per cage	9.22 $\pm$ 1.83	4.11 $\pm$ 1.46	3.30	8	0.006
Eggs per cage	390.89 $\pm$ 146.98	153.78 $\pm$ 62.07	2.39	8	0.022
Neonates per cage	139.22 $\pm$ 69.37	39.22 $\pm$ 23.69	2.03	8	0.039

*A. graveolens* (egg-clusters:  $F = 0.80$ ,  $df = 2$ ,  $P = 0.48$ ; eggs:  $F = 0.33$ ,  $df = 2$ ,  $P = 0.73$ ; neonates:  $F = 0.18$ ,  $df = 2$ ,  $P = 0.84$ ). Although these trials are based on two females per replicate, in all replicates more eggs were laid on *C. murale*. Because of the consistency among replicates, the bias in oviposition is not likely to be the result of random females preferring *C. murale*, and other females preferring *A. graveolens*. Therefore we concluded that, in the greenhouse, *S. exigua* prefer to oviposit on *C. murale* rather than on *A. graveolens*.

**Developmental test.** *Spodoptera exigua* larvae (at days 3 to 9) and pupae were significantly heavier when fed *A. graveolens* than *C. murale* (Table 2). The larvae also required more time to develop on *C. murale* ( $21.3 \pm 1.0$  days) than on *A. graveolens* ( $16.5 \pm 0.4$  days) ( $X^2 = 16.05$ ,  $df = 1$ ,  $P = 0.0001$ ). There were no differences in the days required for development of pupae into adults (*C. murale*:  $7.7 \pm 0.2$  days; *A. graveolens*:  $7.5 \pm 0.1$  days) ( $X^2 = 0.45$ ,  $df = 1$ ,  $P = 0.50$ ).

The relative larval growth rate from 3 to 9 days on *A. graveolens* ( $0.59 \pm 0.01$  mg/mg larva/day) was greater than the relative growth rate on *C. murale* ( $0.50 \pm 0.02$  mg/mg larva/day) ( $X^2 = 17.63$ ,  $df = 1$ ,  $P = 0.0001$ ). Finally, *S. exigua* had a significantly greater survival on *A. graveolens* (60.2%) than on *C. murale* (12.7%) ( $F = 49.37$ ,  $df = 1$ ,  $P < 0.006$ ). These results lead us to reject the working hypothesis that *C. murale* is a superior food source for *S. exigua* development.

## Discussion

Our present results, coupled with previous studies (Berdegué & Trumble, 1996) indicate that neither female oviposition nor larval feeding preference of *S. exigua* are positively correlated with larval performance. The evidence that *S. exigua* prefer to oviposit on *C. murale* rather than on *A. graveolens* and previous results from choice tests with whole plants and leaf discs indicating that the highly mobile *S. exigua*

larvae strongly prefer *C. murale* over *A. graveolens* (Berdegué & Trumble, 1996) are in agreement with observations indicating that *S. exigua* eggs and larvae commonly occur on *C. murale* plants within *A. graveolens* fields (Harding, 1976; M. Diawara & J.T.T., unpubl.). However, these preferences for *C. murale* appear difficult to reconcile with the greater larval performance, pupal masses and survival of *S. exigua* when reared on *A. graveolens* than when reared on *C. murale*. Furthermore the positive relationship between pupal mass and adult fecundity in a closely related species, *S. mauritia acronyctoides* Gmelin (Rothschild, 1969) suggests that the fitness of *S. exigua* when reared on *A. graveolens* would be substantially higher than its fitness when reared on *C. murale*. Therefore, we reject the hypothesis that the preferred *C. murale*, when compared with *A. graveolens*, is a superior host plant for *S. exigua* development.

A lack of correlation between adult host-plant selection and larval suitability has been previously reported (Remington, 1952; Straatman, 1962; Wiklund, 1975; Chew, 1977; Rodman & Chew, 1980; Courtney, 1981, 1982; Singer, 1984; Legg et al., 1986; Karban & Courtney, 1987; Auerbach & Simberloff, 1989; Fox & Eisenbach, 1992; Singer et al., 1994). However, these earlier reports, with the exception of Chew (1977) and Rodman & Chew (1980), describe systems where host plant selection is limited to the adult stage. For *S. exigua*, which has highly mobile larvae (Griswold & Trumble, 1985), there is a lack of correlation for both oviposition and larval feeding preference with larval performance. Both adults and the highly mobile larvae select the inferior host plant, in terms of nutrition, for development.

Rausher (1982) and Futuyma & Slatkin (1983) stated that qualitative differences among hosts of highly polyphagous insects, such as *S. exigua*, can affect herbivore fitness. While the definition for fitness can be variable, there is general agreement that, for most insect species, increasing developmental rate,

Table 2. Developmental parameters of *S. exigua* reared on *C. murale* or *A. graveolens*

	<i>C. murale</i> (mean $\pm$ SE)	<i>A. graveolens</i> (mean $\pm$ SE)	Test statistic	df	P value
Mass 3 days after emergence (mg)	0.43 $\pm$ 0.04	0.61 $\pm$ 0.05	F = 8.90	1	0.003
Mass 4 days after emergence (mg)	0.90 $\pm$ 0.08	1.19 $\pm$ 0.09	F = 7.20	1	0.008
Mass 5 days after emergence (mg)	2.04 $\pm$ 0.23	2.89 $\pm$ 0.32	F = 5.19	1	0.024
Mass 6 days after emergence (mg)	3.94 $\pm$ 0.46	5.90 $\pm$ 0.54	F = 9.75	1	0.002
Mass 7 days after emergence (mg)	7.16 $\pm$ 0.97	11.36 $\pm$ 1.45	F = 7.68	1	0.006
Mass 9 days after emergence (mg)	21.09 $\pm$ 2.94	41.37 $\pm$ 5.10	F = 13.68	1	<0.0001
Pupal mass (mg)	60.09 $\pm$ 2.88	109.62 $\pm$ 3.09	X <sup>2</sup> = 25.78	1	<0.0001

survival and reproductive potential will increase fitness. For *S. exigua* in the system we tested, each of these key factors affecting fitness was influenced by the choice of host.

**Developmental test.** The differences in developmental rates between larvae reared on *C. murale* and *A. graveolens* apparently are not the result of differences in major nutritional factors such as nitrogen or water content that would favor *C. murale* (Berdegué & Trumble, 1996). Because not all possible nutritional components of both species were tested, a final determination that nutritional factors were not involved in larval choice can not be made. However, there is no behavioral evidence from larvae of a feeding stimulant from *C. murale* or a feeding deterrent effect of healthy *A. graveolens*. Older *S. exigua* larvae are deterred from feeding by high levels of linear furanocoumarins found in older foliage of *A. graveolens*, but they show no such sensitivity to the lower concentrations found in the petioles (Berdegué et al., 1997) where the older larvae tend to feed (Griswold & Trumble, 1985). In addition, low concentrations of linear furanocoumarins do not impact development, survival or fitness of *S. exigua* (Brewer et al., 1995; Reitz & Trumble, 1997). Moreover, these hosts do not differ in their attractiveness to *S. exigua* when ground and incorporated in artificial diet (Berdegué & Trumble, 1996).

The rejection of our working hypothesis indicates that host selection is not molded by the food quality of the host plant in this system. Alternative hypotheses may account for the lack of correlation in preference and performance, and can be used to generate predictions of why expected correlations are not observed. In a seminal review, Thompson (1988) discusses four general hypotheses of selection pressures that could act, independently or in concert, to shape host plant

use by an insect herbivore species and explain existing patterns of oviposition preference and larval performance: a time hypothesis; a patch dynamics hypothesis; a parasite/grazer hypothesis; and an enemy-free space hypothesis.

According to the time hypothesis, females may oviposit on unsuitable novel hosts, and these ovipositions may persist because there has been insufficient evolutionary time for female oviposition preferences to shift from these unsuitable, novel hosts. The genus *Apium* consists of approximately 20 spp. and is distributed around the world (Ochoa & Quiros, 1989). Although its center of origin remains unknown, it is believed to have originated in the Mediterranean region, possibly in the Italian peninsula (Quiros, 1993). The genus *Chenopodium* also has a worldwide distribution. *C. murale* is believed to have originated in the Andean region of South America (Risi & Galwey, 1984). *S. exigua* originated in southern Asia and was first reported in California in 1882 (Wilson, 1932). Hence, the association of this herbivore with both *C. murale* and *A. graveolens* in California is approximately 110 years old. Although one hundred years has been sufficient time for the oviposition preference of *Euphydryas editha* (Taylor) to shift to a suitable novel host, its larval performance has not improved on the new host (Thomas et al., 1987). Conversely, Chew (1977) and Rodman & Chew (1980) found that *Pieris* populations did not eliminate indiscriminate oviposition behavior within 100 years after a lethal host, *Thlaspi arvense* L., was introduced into North America (but see Jones, 1977). Yet, *Pieris* females ignore *Erysimum asperum* (Nuttall), a native plant, for oviposition, probably because of its lethal effects on the larvae (Chew, 1977). Remington (1952), Straatman (1962), Wiklund (1975), and Legg et al. (1986) also have documented similar cases

where a negative relationship between host preference by adult lepidopterans and larval performance results from a lack of evolutionary history. Herbivore populations that are undergoing rapid evolution in preferences may not show a correlation or concordance between preference and performance, but concordance between these traits is expected in stable populations (i.e., populations not undergoing rapid preference evolution, Singer et al., 1994). Therefore, we cannot exclude the possibility that the association of *S. exigua* with *A. graveolens* and *C. murale* is too recent for preference to correspond with performance.

If time were the only factor accounting for the discrepancies in preference and performance, we would expect a trend for either greater numbers of ovipositions to occur on *A. graveolens* (see Karowe, 1990) or increased larval preference for *A. graveolens* (see Singer et al., 1994). However if, as Futuyma & Slatkin (1983) argue, preference can evolve before larval performance, our results would lead to a prediction that performance of *S. exigua* on *C. murale* should increase over time.

Thompson's second hypothesis, the patch dynamics hypothesis predicts that females will oviposit disproportionately more on hosts that they encounter more frequently. This hypothesis appears unlikely to account for the host preferences of *S. exigua*. *A. graveolens* is grown in large monocultures in California (Koike et al., 1996) with *C. murale* being an incidental weed in those agroecosystems. Despite such an overwhelming predominance of *A. graveolens*, *C. murale* is the preferred plant for oviposition and larval feeding.

The parasite/grazer hypothesis predicts that grazers (i.e., herbivores that can complete development on more than one host) are not as likely to show strong host plant oviposition preferences as parasitic herbivores (i.e., herbivores that complete development on one host plant). Thompson (1988) further postulated that females of grazer species could oviposit preferentially on hosts that yield greater survivorship of eggs, and then older larvae could move to more nutritionally superior hosts. Such a scenario is not likely for *S. exigua* because females prefer *C. murale* for oviposition, and we found no difference in the hatching success of eggs on these two host plants. Furthermore older larvae also prefer to feed on *C. murale* (Berdegué & Trumble, 1996), and all larval stages can be found feeding on *C. murale* in the field (Harding, 1976; M. M. Diawara & J.T.T., unpubl.).

The enemy free space hypothesis predicts that herbivores may prefer nutritionally inferior host plants if those inferior hosts afford greater protection from natural enemies than nutritionally superior hosts (see Fox & Eisenbach, 1992). Ultimately the increase in fitness resulting from that protection must compensate for any fitness reduction resulting from development on the nutritionally inferior host (Berdegué et al., 1996). Development on *C. murale* does represent a fitness cost for *S. exigua*. In particular, *S. exigua* experiences greater mortality when reared on *C. murale* than when reared on *A. graveolens*. Therefore, we predict that for enemy free space to select for *C. murale* preference, location of *S. exigua* by natural enemies would be inhibited substantially on *C. murale*, or that insect pathogens are more virulent on *A. graveolens* than on *C. murale*. While no information is available on host location by natural enemies of *S. exigua* on these particular plants, there is evidence that host plants can affect the discovery of herbivores by natural enemies (Kester & Barbosa, 1991; Fox & Eisenbach, 1992; Benrey & Denno, 1997), virulence of viruses attacking *Spodoptera* species (Richter et al. 1987), and that pathogenicity of the bacteria, *Bacillus thuringiensis* Berliner, is enhanced by some compounds found in *A. graveolens* (Berdegué & Trumble, 1997).

In summary, *S. exigua* adults and larvae prefer *C. murale* to *A. graveolens* as a host plant. Host plant selection in this system is not governed by the food quality of the host plant. It is possible that the observed preference for the less suitable host is the result of the recent association of these three species in agroecosystems in North America. Alternatively, host plant preference for oviposition and larval development could be a result of enemy free space, and mother and offspring may 'know best' by considering factors other than strict nutritional quality of host plants.

### Acknowledgements

We thank K. White, S. Young, G. Kund, M. White, and W. Carson for their technical assistance. The reviews of an earlier draft of this manuscript by C. Coviella, J. D. Hare, J. Millar, C. Rodriguez-Saona, P. K. Visscher, and M. Zalucki are appreciated. This research was supported, in part, by USDA grant 95373121634, the California Celery Research Advisory Board, the California Tomato Commission, and CONACYT Mexico.

## References

- Auerbach, M. & D. Simberloff, 1989. Oviposition site preference and larval mortality in a leaf-mining moth. *Ecological Entomology* 14: 131–140.
- Benrey, B. & R. F. Denno, 1997. The slow-growth-high-mortality hypothesis: A test using the cabbage butterfly. *Ecology* 78: 987–999.
- Berdegú, M. & J. T. Trumble 1996. Effects of plant chemical extracts and physical characteristics of *Apium graveolens* and *Chenopodium murale* on host choice by *Spodoptera exigua* larvae. *Entomologia Experimentalis et Applicata* 78: 253–262.
- Berdegú, M. & J. T. Trumble. 1997. Interaction between linear furanocoumarins found in celery and a commercial *Bacillus thuringiensis* formulation on *Spodoptera exigua* (Lepidoptera: Noctuidae) larval feeding behavior. *Journal of Economic Entomology* 90: 961–966.
- Berdegú, M., J. T. Trumble, J. D. Hare & R. A. Redak, 1996. Is it enemy free space? – The evidence for terrestrial insects and fresh water arthropods. *Ecological Entomology* 21: 203–217.
- Berdegú, M., K. K. White & J. T. Trumble, 1997. Feeding deterrence of *Spodoptera exigua* (Lepidoptera: Noctuidae) larvae by low concentrations of linear furanocoumarins. *Environmental Entomology* 26: 912–919.
- Bernays, E. A. & R. F. Chapman, 1994. *Host-Plant Selection by Phytophagous Insects*, Chapman & Hall, New York.
- Brewer, M. J., T. Meade & J. T. Trumble, 1995. Development of insecticide-resistant and -susceptible *Spodoptera exigua* (Lepidoptera: Noctuidae) exposed to furanocoumarins found in celery. *Environmental Entomology* 24: 392–401.
- Carriere, Y., 1992. Host plant exploitation within a population of a generalist herbivore, *Choristoneura rosaceana*. *Entomologia Experimentalis et Applicata* 65: 11–19.
- Chew, F. S., 1977. Coevolution of pierid butterflies and their cruciferous foodplants. II. The distribution of eggs on potential foodplants. *Evolution* 31: 568–579.
- Courtney, S. P., 1981. Coevolution of pierid butterflies and their cruciferous foodplants: III. *Anthocharis cardamines* (L). survival, development and oviposition on different host plants. *Oecologia* 51: 91–96.
- Courtney, S. P., 1982. Coevolution of pierid butterflies and their cruciferous foodplants: V. Habitat selection, community structure and speciation. *Oecologia* 54: 101–107.
- Damman, H. & P. Feeney, 1988. Mechanisms and consequences of selective oviposition by the zebra swallowtail butterfly. *Animal Behavior* 36: 563–573.
- Diawara, M. M., J. T. Trumble, C. F. Quiros & J. G. Millar, 1992. Resistance to *Spodoptera exigua* in *Apium prostratum*. *Entomologia Experimentalis et Applicata* 64: 125–133.
- Diawara, M. M., J. T. Trumble, M. L. Lacy, K. K. White & W. G. Carson, 1996. Potential of somaclonal celeries for use in integrated pest management. *Journal of Economic Entomology* 89: 218–223.
- Eigenbrode, S. D., J. T. Trumble & R. A. Jones, 1993. Resistance to beet armyworm, hemipterans, and *Liriomyza* spp. in *Lycopersicon* accessions. *Journal of American Society Horticultural Science* 118: 525–530.
- Fox, L. R. & J. Eisenbach, 1992. Contrary choices: possible exploitation of enemy-free space by herbivorous insects in cultivated vs. wild crucifers. *Oecologia* 89: 574–579.
- Futuyma, D. J., & M. Slatkin, 1983. *Coevolution*, Sinauer Associates, Sunderland, Massachusetts.
- Griswold, M. J. & J. T. Trumble, 1985. Responses of *Spodoptera exigua* (Lepidoptera: Noctuidae) larvae to light. *Environmental Entomology* 14: 650–653.
- Harding, J. A., 1976. *Heliothis* spp.: parasitism and parasites plus host plants and parasites of the beet armyworm, diamondback moth and two tortricids in the lower Rio Grande Valley of Texas. *Environmental Entomology* 5: 669–671.
- Jones, R. E., 1977. Search behavior: a study of three caterpillar species. *Behaviour* 60: 237–259.
- Karban, R. & S. Courtney, 1987. Intraspecific host plant choice: lack of consequences for *Streptanthus tortuosus* (Cruciferae) and *Euchloe hyantis* (Lepidoptera: Pieridae). *Oikos* 48: 243–248.
- Karowe, D. N., 1990. Predicting host range evolution: colonization of *Coronilla varia* by *Colias philodice* (Lepidoptera: Pieridae). *Evolution* 44: 1637–1647.
- Kester, K. M. & P. Barbosa, 1991. Behavioral and ecological constraints imposed by plants on insect parasitoids: implications for biological control. *Biological Control* 1: 94–106.
- Koike, S. T., K. F. Schulbach & W. E. Chaney, 1996. Celery production in California, University of California Division of Agricultural and Natural Resources, Report 7220.
- Legg, D. E., T. C. Schenk & H. C. Chang, 1986. European corn borer (Lepidoptera: Pyralidae) oviposition preference and survival on sunflower and corn. *Environmental Entomology* 15: 631–634.
- Nylin, S. & N. Janz, 1993. Oviposition preference and larval performance in *Polygonia c-album* (Lepidoptera: Nymphalidae): the choice between bad and worse. *Ecological Entomology* 18: 394–398.
- Nylin, S. & N. Janz, 1996. Host plant preferences in the comma butterfly (*Polygonia c-album*): Do parents and offspring agree? *Ecoscience* 3: 285–289.
- Ochoa, O. & C. F. Quiros, 1989. *Apium* wild species: novel sources for resistance to late blight in celery. *Plant Breed* 102: 317–321.
- Patana, R., 1969. Rearing cotton insects in the laboratory. Report. Number. 108. USDA Production Research Report. Number 108, 6 pp.
- Quiros, C. F., 1993. Celery *Apium graveolens* L. In: G. Kalloo & B. O. Bergh (eds), *Genetic Improvements of Vegetable Crops*. Pergamon Press, New York, pp. 523–534.
- Rausher, M. D., 1982. Population differentiation in *Euphydryas editha* butterflies: larval adaptation to different hosts. *Evolution* 36: 581–590.
- Rausher, M. D. & D. R. Papaj, 1983. Demographic consequences of discrimination among conspecific host plants by *Battus philenor* butterflies. *Ecology* 64: 1402–1410.
- Reitz, S. R. & J. T. Trumble, 1997. Effects of linear furanocoumarins on the herbivore *Spodoptera exigua* and the parasitoid *Archytas marmoratus*: Host quality and parasitoid success. *Entomologia Experimentalis et Applicata* 84: 9–16.
- Remington, C. L., 1952. The biology of nearctic Lepidoptera - I. Foodplants and life histories of Colorado Papilionoidea. *Psyche* 59: 61–70.
- Richter, A. R., J. R. Fuxa & M. Abdel-Fattah, 1987. Effect of host plant on the susceptibility of *Spodoptera frugiperda* (Lepidoptera: Noctuidae) to a nuclear polyhedrosis virus. *Environmental Entomology* 16: 1004–1006.
- Risi, J. & N. W. Galwey, 1984. The *Chenopodium* grains of the Andes: Inca crops for modern agriculture. *Advances in Applied Biology* 10: 145–216.
- Rodman, J. & F. S. Chew, 1980. Phytochemical correlates of herbivory in a community of native and naturalized Cruciferae. *Biochemical Systematics and Ecology* 8: 43–50.

- Rothschild, G. H. L., 1969. Observations on the armyworm *Spodoptera mauritia acronyctoides* Gn. (Lep., Noctuidae) in Sarawak (Malaysian Borneo). *Bulletin of Entomological Research* 59: 143–160.
- SAS, 1990. Users' Guide: Statistics, 4 edition, vol 1, SAS Institute, Cary, NC.
- Scriber, J. M. & F. Slansky, Jr., 1981. The nutritional ecology of insects. *Annual Review of Entomology* 26: 183–211.
- Singer, M. C., 1984. Butterfly-host plant relationships: host quality, adult choice and larval success. In: R. Vane-Wright & P. R. Ackery (eds.), *The biology of butterflies*. Academic Press, New York, pp. 81–88.
- Singer, M. C., C. D. Thomas, H. L. Billington & C. Parmesan, 1994. Correlates of speed of evolution of host preference in a set of twelve populations of the butterfly *Euphydryas editha*. *Ecoscience* 1: 107–114.
- Smits, P. H., M. C. van Velden, M. van deVrie & J. M. Vlask, 1987. Feeding and dispersion of *Spodoptera exigua* larvae and its relevance for control with a nuclear polyhedrosis virus. *Entomologia Experimentalis et Applicata* 43: 67–72.
- Sokal, R. R. & F. J. Rohlf, 1995. *Biometry: the Principles and Practice of Statistics in Biological Research*, 3rd. ed. Freeman, New York.
- Straatman, R., 1962. Notes on certain Lepidoptera ovipositing on plants which are toxic to their larvae. *Journal of Lepidopterists' Society* 16: 99–103.
- Thomas, C. D., D. Ng, M. C. Singer, J. L. B. Mallet, C. Parmesan & H. L. Billington, 1987. Incorporation of a European weed into the diet of a North American herbivore. *Evolution* 41: 892–901.
- Thompson, J. N., 1983. The use of ephemeral plant parts on small host plants: how *Depressaria leptotaeniae* (Lepidoptera: Oecophoridae) feeds on *Lomatium dissectum* (Umbelliferae). *Journal of Animal Ecology* 52: 281–291.
- Thompson, J. N., 1988. Evolutionary ecology of the relationship between oviposition preference and performance of offspring in phytophagous insects. *Entomologia Experimentalis et Applicata* 47: 3–14.
- Van Steenwyk, R. A. & N. C. Toscano, 1981. Relationship between lepidopterous larval density and damage in celery and celery plant growth analysis. *Journal of Economic Entomology* 74: 287–290.
- White R. R. & M. C. Singer, 1974. Geographical distribution of hostplant choice in *Euphydryas editha* (Nymph.) *Journal of Lepidopterists' Society* 28: 103–107.
- Wiklund, C., 1975. The evolutionary relationship between adult oviposition preferences and larval host plant range in *Papilio machaon* L. *Oecologia* 18: 185–197.
- Wiklund, C., 1984. Egg-laying patterns in butterflies in relation to their phenology and the visual apparency and abundance of their host plants. *Oecologia* 63: 23–29.
- Wilson, J. W., 1932. Notes on the biology of *Laphygma exigua* Hübner. *Florida Entomologist* 16: 33–39.