Is diamondback moth a polyphagous pest? Some thoughts about its host range expansion to pea

S. Subramanian and Bernhard Löhr

Plant Health Division, International Center of Insect Physiology and Ecology (ICIPE), P. O. Box 30772-00100, Nairobi, Kenya
Corresponding author: ssuramania@icipe.org, subbisyv@rediffmail.com

ABSTRACT

The diamondback moth (DBM), *Plutella xylostella* L. (Lepidoptera: Plutellidae), has been recognized as an oligophagous pest feeding on more than 40 wild and cultivated crucifers. However they have occasionally been recorded on some non-crucifers. The first field level observation of this pest on pea was made in the Naivasha region of Kenya in 1999. Furthermore, a population collected from cabbage was even able to adapt to survive on pea for four generations. Oviposition and larval preference experiments were conducted with naïve field populations collected from cabbage fields in Naivasha with a laboratory-reared pea-adapted population as a check. Both under choice and no-choice conditions, both populations preferred cabbage over pea for oviposition and larval survival. However, under no-choice test condition, the Naivasha population preferred pea for laying 33.7% of the eggs laid on cabbage under similar conditions. Among the pea plant parts, the leaf auricle was preferred for oviposition over the leaf lamina, tendril and stem. Pea leaf discs were also preferred by 26.7% of the neonate larvae of the Naivasha population under no-choice test condition. Under no-choice condition, the pea-adapted population moths and larvae equally preferred cabbage and pea for oviposition and larval survival. The increased oviposition preference on pea, sitedirected oviposition on pea leaf auricles and neonate larval preference for pea indicate that the ability to survive on pea is a characteristic of the Naivasha population. Does the occasional observation on non-crucifers have any genetic or chemical basis? Does this ability to survive on pea exist in other DBM populations as well? The results are discussed in light of host range expansion of DBM and its implications on the selection of this insect as a model for further studies on the phenomenon of sympatric speciation.

INTRODUCTION

Insects are broadly categorized, based on their host range, as monophagous, oligophagous or polyphagous. Monophagous insects thrive only on plants belonging to a single species and they select their host plant based on specific characteristics of the plant. For example, the carrot root fly, *Psila rosae*, is attracted to *trans*-asarone, a volatile compound specific to carrot. Oligophagous insects feed upon a few plants belonging to a single family or on plants related by a narrow suite of characteristics, as with *Plutella xylostella* (L.), which preferably feeds on plants belonging to cruciferae. The latter is also referred to as “disjunct oligophagy”. The host range of polyphagous insects include a wide array of plants belonging to different families and there are very few common features among the plants which govern the selection of such plants by insects (Bernays and Chapman 1994).
Polyphagous and oligophagous pests, in the absence or decreased abundance of host plants within their normal host range, may also adapt to novel hosts closely related to their original hosts (Scriber and Ording 2005, Gutierrez and Thomas 2000). However, such host-range expansions or host shifts would involve several changes in the genetic (Thomas et al. 2003, Nygren et al. 2006), behavioral (Grassman et al. 2006) and physiological insect characteristics (Tallamy 2000), such as altered oviposition behavior of the females towards the novel hosts, larval acceptance and ability of the larvae to assimilate the deterrent chemicals in the novel hosts for their development.

Such host range expansion could be advantageous to some insect pests when the natural enemies specialized to locate the pest in the original host are not able to locate them on the novel hosts. Such a phenomenon creates an “enemy-free space” for the pest to thrive on the novel hosts (Rossbach et al. 2006).

A number of such host shifts or host range expansions by insects have been reported in biological weed control programs (Marohasy 1996) and in introduction of invertebrate biocontrol agents (Pimentel et al. 1984). There are few reports on host range expansion in phytophagous insect pests, except in cases of accidental introduction of a pest into a new geographical location. However there are extensive studies on the development of biotypes in crop pests, which are capable of breaking the resistance offered by the resistant cultivars.

*Plutella xylostella*: a worldwide menace

The diamondback moth (DBM), *P. xylostella*, is a cosmopolitan and destructive pest on crucifers. It is oligophagous and thrives well on cultivated crucifers including cabbage, cauliflower, canola, mustard and also on some wild crucifers like *Raphanus raphanistrum*, *Rorippa* sp., *Erucastrum arabicum* etc. Estimated crop losses caused by this pest in different parts of the world annually are ca US $ 16 million in India (Mohan and Gujar 2003a), ca US $ 40-70 million for cabbage and US $ 0.4 million for broccoli crop in Texas (Shelton 2004). DBM outbreaks could cause as much as 90% crop loss in Southeast Asia (Verkerk and Wright 1996), 52% yield loss on cabbage in India (Krishnamoorthy 2004), 80%-99% damage of summer cabbage in China (Zhao et al. 1996) and 12-48.7 tons/ha of cabbage heads in Ethiopia (Ayalew 2006).

The worldwide distribution and remarkable damage potential of this pest is attributed to the diversity and abundance of its host plants, its high reproductive rate and short life span (over 20 generations per year in the tropics). In addition, its genetic elasticity facilitates rapid development of resistance to a wide range of insecticides (Mohan and Gujar 2003b, Shelton 2004).

Occurrence on non-cruciferous hosts

The host range of DBM has not always been restricted to the crucifers and it has been occasionally recorded on plants belonging to other families like Capparadaceae (Sarfraz et al. 2005), Fabaceae (Löhr 2001, Reichardt 1919), Amaranthaceae (Vishakanthiah and Visweshwara Gowda 1975), Chenopodiaceae (Reichardt 1919) and Malvaceae (Gupta 1971).

Host range expansion of *Plutella xylostella* on peas

Insects do undergo expansions in their host ranges or shifts in their host preference due to several reasons like climatic changes (Thomas et al. 2001, Root et al. 2003, Battisti et al. 2005) and habitat expansion caused by man, as in the case of introduced pests or weed biological control programmes (Gutierrez and Thomas 2000). Some of the host range expansion by *P. xylostella* to non-crucifers occurred when the previous crucifer crop was completely devastated and a novel host was planted in the vicinity (Löhr 2001, Löhr and Gathu 2002, Gupta 1971). Such a phenomenon indicates that the initial oviposition onto the novel host was due to the non-availability of the preferred host and was not a preferential event. DBM moths
from populations that persist at high densities are more generalized in food plant use than moths from low-density populations (Bigger and Fox 1997) and the dispersal ability of DBM on its own is generally limited (Shirai and Nakamura 1994). although wind can carry them through great distances (Chu 1986).

However, the cruciferous ecosystem in Kenya has a rich diversity of wild crucifers and cultivation of crucifers is widespread, both as small farmers’ fields, home gardens and large scale export oriented farms (Gathu et al. 2006). Cruciferous vegetables like cabbage and kale are principal vegetables of the Kenyan diet, resulting in their widespread cultivation. Recently Zhang and Liu (2006) reported that experience of nonhost plant like peas by DBM may alter their foraging and oviposition response to peas, and naïve populations did not accept pea for oviposition in either no-choice or choice conditions. Further Liu and Liu (2006) reported that there was no evidence of preimaginal conditioning, but a strong effect of emergence conditioning and early adult learning on oviposition preference to pea. The host range expansion by Plutella xylostella, in spite of the presence of wild and cultivated crucifers in the vicinity, brings to fore many questions to be answered.

Is there any genetic basis for such a host range expansion?
Is there any chemical basis for the selection of snow pea plants by Plutella xylostella?
Is this host range expansion to pea a localized phenomenon of the DBM population in Naivasha, Kenya?
Is the electrophysiological perception characteristic of the Naivasha population different from others?
Would this have been detected in a host specificity screening?

In this regard, oviposition and larval preference experiments were conducted in our laboratory with a naïve field-collected population from the Naivasha region of Kenya as an initial step of providing answers to some of these questions.

MATERIALS AND METHODS

Oviposition preference

Oviposition preference experiments were conducted in our laboratory with 30 day-old potted pea and 45 day-old cabbage plants under choice and no-choice test conditions, with a naïve field-collected population from cabbage crops in Naivasha region. A pea-adapted population reared continuously on pea for over 60 generations was also used for comparison. Mated adult DBM pairs of both the populations were released into cages (1 m x 0.6 m x 0.6 m) at the rate of one pair per potted plant. Each cage for the no-choice experiments had either four potted pea or cabbage plants. In the choice experiments each cage had two plants each of cabbage and pea. The number of eggs laid on different plant parts of both cabbage and pea were recorded 48 hours after the release of the insects.

Larval preference

Larval preference of neonates emerging from eggs laid by the Naivasha population and the pea-adapted population females were evaluated under no-choice and choice test conditions in the laboratory.

A no-choice larval preference test was conducted in the laboratory with pea, cabbage and swiss chard (neutral non-host) leaf discs (2.5 cm) placed radially in Petri dish. Six leaf discs were placed per Petri dish. The leaf discs were placed over a layer of moist filter paper to maintain their turgidity. Ten neonate larvae per Petri dish were released at the centre of the Petri dish and allowed to select the leaf discs. The number of insects settled on each leaf disc was observed after 24 hours. Each treatment was replicated three times.

Statistical analysis

Comparison of mean number of eggs laid on cabbage and pea under no-choice test and the larval
preference percentage for the different host leaf discs were performed using two factors ANOVA, with the population and host plants as factors. Means were separated by Tukey’s studentised range (HSD) test. The mean numbers of eggs laid on different pea plant parts were compared with Kruskal-Wallis nonparametric ANOVA (SAS institute, 2001). In the choice tests, the mean number of eggs laid on different plants by different populations were compared using Student’s t-test.

■ RESULTS ■

Oviposition preference

Cabbage was the preferred host for oviposition both under choice \( (P = 0.02, \text{ Student's } t\text{-Test}) \) and no-choice test conditions \( (F = 27.31, df = 1, 12; P = 0.002, \text{ Two factor ANOVA}) \) (Table 1). Considering the number of eggs deposited on cabbage to be the normal level of oviposition, this population of DBM, even with no previous exposure to peas, laid 33.75% of eggs on snow peas in the no-choice test situation (Table 1). The pea-adapted population equally preferred both cabbage and pea for oviposition under no-choice condition. Both the populations tested preferred to oviposit on the leaf auricles rather than on the leaf lamina, tendrils and stems \( (F = 13.718 \, 6, df = 3, P = 0.003 \, 3; \text{ Non Parametric One Way ANOVA}) \) (Figure 1).

Larval preference

The neonate larvae of both the Naivasha and pea-adapted populations also preferred cabbage leaf discs over pea \( (P < 0.000 \, 1) \) and swiss chard \( (P < 0.000 \, 1) \) leaf discs in choice and no-choice tests \( (F = 41.43, df = 2, 12; P < 0.000 \, 1, \text{ Two Factors ANOVA}) \) (Table 2). Cabbage and swiss chard leaf discs were equally preferred by both the Naivasha and the pea adapted population under choice \( (P = 0.34, \text{ cabbage}; P = 0.18, \text{ swiss chard}; \text{ Student's } t\text{-test}) \) and no-choice test conditions \( (P = 0.92, \text{ cabbage}; P = 0.99, \text{ swiss chard}; \text{ Two Factors ANOVA}) \). The preference for the pea leaf discs was significantly higher by the pea-adapted population than the Naivasha population under choice \( (P = 0.053) \) and no-choice tests \( (P = 0.02) \). Under no-choice situation, 27% of the larvae preferred to feed on pea leaf discs.

![Figure 1 Oviposition preference of different diamondback moth populations for parts of pea plant. Bars are means ± SE](image-url)
Table 1  Oviposition preference of the Naivasha population (F₀) and a pea-adapted (laboratory) strain of diamondback moth towards pea and cabbage

<table>
<thead>
<tr>
<th>Population</th>
<th>Mean no. of eggs laid per potted plant</th>
<th>No. of eggs laid per female in</th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Cabbage</td>
<td>Pea</td>
<td>Cabbage</td>
</tr>
<tr>
<td>Naivasha population (F₀)</td>
<td>85.5 ± 9.6 Aa</td>
<td>0.5 ± 0.35 Bb</td>
<td>40.8 ± 1.99 Aa</td>
</tr>
<tr>
<td>Pea-adapted population</td>
<td>31.5 ± 3.89 Bb</td>
<td>2.5 ± 0.35 Ab</td>
<td>15 ± 0.93 Bb</td>
</tr>
</tbody>
</table>

* In a column, means followed by different letters in upper case indicate significant difference among the populations by Tukey HSD test (P ≤ 0.05). In a row, means followed by different letters in lower case indicate significant difference among the host plants by Tukey HSD test (P ≤ 0.05).

Table 2  Preference of neonate larvae of the Naivasha population (F₀) and a pea-adapted (laboratory) strain of diamondback moth towards pea, cabbage and swiss chard

<table>
<thead>
<tr>
<th>Population</th>
<th>Mean larval preference percentage</th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Cabbage</td>
<td>Pea</td>
</tr>
<tr>
<td>Naivasha population (F₀)</td>
<td>63.3 ± 5.6 Aa</td>
<td>1.7 ± 1.67 Bb</td>
</tr>
<tr>
<td>Pea adapted population</td>
<td>58.3 ± 10.1 Aa</td>
<td>20.0 ± 9.3 Ab</td>
</tr>
</tbody>
</table>

* In a column, means followed by different letters in upper case indicate significant difference among the populations by Tukey HSD test (P ≤ 0.05). In a row, means followed by different letters in lower case indicate significant difference among the host plants by Tukey HSD test (P ≤ 0.05).

** DISCUSSION **

Plasticity in host acceptance is an important factor in host specialization of phytophagous insects. Knowledge of the underlying genetic coding of this and other antecedent behaviours, e. g. host location, is necessary in order to understand how host shifts occur (Hora et al. 2005). While DBM predominately specializes on feeding and ovipositing on cruciferous plants, it was recently recorded on peas in a field at Naivasha in Kenya (Löhr 2001, Löhr and Gathu 2002). Further, preimaginal experience of the female moth to pea has been reported to increase the oviposition preference to the non-host (Zhang and Liu 2006, Liu and Liu 2006). The results of the present study has shown that a naïve field population collected from cabbage fields in the Naivasha region laid 33.7% of eggs on snow peas even with no prior experience to the non-host (Table 1). This is in contrast to the findings of Zhang and Liu (2006) that naïve DBM moths with no prior experience laid only 1.5% of eggs on pea plants, as compared to the eggs laid on Chinese cabbage under no-choice test condition. Even females subjected to prior experience of pea oviposited only up to 20% of their eggs on pea plants.

The difference in the preference for pea plants might be due to population differences. Allozyme frequency analysis on fourteen different populations collected worldwide showed that they were genetically diverse (Pichon et al. 2006). The DBM moths tested also preferred to lay their eggs on the leaf auricle compared to the leaf lamina, tendril and stem (Figure 1). This indicates that host selection process on peas by the DBM population tested is not due to inappropriate landing (Finch and Golnier 2000) or due to the plant
position effect (Couty et al. 2006), but involves both the chemosensory and tactile stimuli from the plants.

In the larval host plant preference study, pea was more preferred by the pea-adapted population when compared to the Naivasha population. However 26.7 percent of the Naivasha population neonates also settled on peas under no-choice test condition. Hence we suggest that the oviposition and larval preference of the DBM population from Naivasha towards pea is not an experience-induced event but rather a characteristic of the population.

The earliest observation of the ability of survival of DBM larvae on pea was by Gupta and Thorsteinson (1960 a, h). They observed that DBM larvae could be reared on a variety of leguminous plants, but survival significantly improved when they were allowed to feed for the first 10-12 hours on mustard or sinigrin-treated legume leaf surface to stimulate feeding. Detailed evaluation of the ability of a DBM population collected earlier from cabbage fields in the Juja region to adapt to peas revealed that larval survival increased from 2.4%-49.7% in four generations (Löhr and Gathu 2002). This suggested that pea was nutritionally adequate for the larval development of DBM; however, the sequential increase in the survival over subsequent generations indicate the possibility of a genetic linkage for such survival on a non-host. The pea-adapted population is also genetically diverse from other DBM populations collected from different parts of the world and the “survival on peas” trait was maternally linked (Janssen 2006).

The results of the present and previous studies (Löhr and Gathu 2002, Janssen 2006) provide evidence that the ability of the DBM population to expand its host range to peas is a population characteristic. However, it is necessary to evaluate other populations of DBM from different geographical regions for similar host range expansion characteristics. Colonization of novel host plants is an evolutionary process that is capable of generating new variation in host use, and could thus conceivably be the “missing fuel” in the engine of diversification (Janz et al. 2005, Nylin et al. 2005).

The outcome of such an evaluation can yield information on the diversity of *P. xylostella* populations with regards to their host plant use, factors that facilitate host shifts in monophagous or oligophagous weed biocontrol agents, and bioassay procedures to be adopted for safety testing of such biocontrol agents before their release. Ability to colonize novel hosts occurs occasionally in insect species and this is considered an important factor promoting insect speciation. However the main hurdle in studying the inheritance of host use is the lack of suitable biological systems (Hora et al. 2005). The advantages of the short life cycle, high reproductive capacity, amenability for laboratory rearing and the genetic elasticity associated with DBM makes it an ideal insect for investigating the phenomenon of sympatric speciation.

The host selection process in the normal crucifer-associated population has been studied in detail, and both chemical (glucosinolates, epicuticular waxes and isothiocyanates) and physical stimuli (leaf colour, leaf texture) have been implicated (Justus and Mitchell 1996, Badenes-Perez et al. 2005, 2006, Eigenbrode and Espelie 1995, Justus et al. 2000). The chemical basis for oligophagy of *P. xylostella* larvae on crucifers has historically been one of the first investigated (van Loon et al. 2002). Do we need to reinvestigate the same in the light of host range expansion onto novel hosts like pea? The question still remains if DBM can be classified as an oligophagous or polyphagous pest. The answers could be obtained only with the detailed investigation on the basis of non-cruciferous host selection by DBM and also on the diversity of populations with regard to their propensity to adapt to the novel host plant.

**Acknowledgements**

We take this opportunity to thank the German Federal Ministry of Economic Cooperation and Development (BMZ) for sponsoring the project through the German Agency of Technical Cooperation (GTZ). We also express our sincere gratitude to Dr. Peter Njagi, sensory biologist, for his critical review of the manuscript.
REFERENCES


Gupta, PD and Thorsteinson, AJ. (1960b) Food plant relationship of the diamondback moth (Platella maculipennis (Curt.)). II. Sensory regulation of oviposition of the adult female. Entomologia Experimentalis et Applicata 3: 305-314.


Hora, KJ, Roessingh, P and Menken, SBJ. (2005) Inheritance and plasticity of adult host acceptance


van Loon, JJA, Wang, CZ, Nielsen, JK, Gols, R and Qiu, YT. (2002) Flavonoids from cabbage are feeding stimulants for diamondback moth larvae additional to glucosinolates: Chemoreception and behaviour. Entomologia Experimentalis et Applicata 104: 27-34.


