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Temperature Effects on the Development of Vietnamese Cotton Bollworm *Helicoverpa armigera* (Hübner)

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Cotton bollworm *Helicoverpa armigera* (Lepidoptera: Noctuidae) is a major pest of cotton, green onion, groundnut, chickpea, tomato, sorghum, cowpea, etc., distributing widely in Asia, Europe and Africa. This pest often causes great economic damage due to its high reproductive potential and pesticide resistance. It is well established that temperature is one of the most important factors in determining the survival, development, and size of insects, but the effects can be modified depending on the geographic strains. Here, we investigated the effects of constant temperatures on the survival, development and individual size of Vietnamese *H. armigera* when reared on bean sprouts in the laboratory. The results showed that the survivals from larval hatching to adult emergence from the pupa were lower under lower temperatures. The duration of the developmental stages decreased as temperature increased from 20°C to 30°C. Developmental thresholds for the eggs, larvae, pupae and life cycle were estimated as 11.5, 13.3, 14.4 and 10.2°C, respectively. Thermal constants for the egg, larval and pupal stages were 45.9, 243.9 and 117.6 degree–days above the developmental thresholds, respectively. A thermal constant of 526.3 degree–days above a threshold of 10.2°C was estimated to be required for the life cycle. The size, measured as pupal weight, increased with rearing temperatures. The results of the present study showed that ca. 30ºC is the optimal temperature for *H. armigera* development and growth. *Helicoperva armigera* may complete a maximum of 10–11 generations per year in Hanoi, Vietnam. The present results provide important information for predicting the field population phenology of *H. armigera* in Hanoi, Vietnam.

Key words: Armyworm, budworm, pest management, corn pests, fitness, Vietnam

INTRODUCTION

Corn is the second most important food crop in Vietnam, next to rice (Ha *et al*., 2004). In Vietnam, several lepidopteran pest species are known to reduce the productivity and quality of corn, e.g., *Ostrinia nubilalis* (Hübner) (European corn borer), *Agrotis ipsilon* (Hufnagel) (Black cutworm) and *Helicoverpa armigera* (Hübner) (cotton bollworm or corn earworm). Among them, *H. armigera* is considered a major serious corn pest in many parts of Africa, Europe, Australia and Asia including Vietnam (Pogue, 2004; Kriticos *et al*., 2015; CABI, 2017). In Vietnam, this lepidopteran is also known to be a significant pest attacking tomato, okra, peanut, pea, green bunching onion, etc. (e.g., Ueno, 2006; Chien and Huong, 2007).

Helicoverpa armigera is listed as an A2 quarantine pest by EPPO, and the annual economic loss due to this pest is estimated to be 2 billion USD or even more (CABI, 2017). The major pest status of *H. armigera* is rooted in its mobility, polyphagy, and high reproductive rate (Fitt, 1989; King, 1994; Pogue, 2004; CABI, 2017). Also, recent studies have demonstrated the successful recent invasion into Central and South America (e.g., Tay *et al*., 2013; Murúa *et al*., 2014), and the incursion into North America may be a matter of time (Kriticos *et al*., 2015); *H. armigera* is now a worldwide important pest. Severity of this pest is often very high because *H. armigera* commonly infests reproductive part of host crops, i.e., flowers and fruits (e.g., Cameron, 1989; Bouchard *et al*., 1992; King, 1994; Jallow *et al*., 2001). Also, because of high level of resistance to many commercialized pesticides and BT, control of *H. armigera* is often difficult solely by chemical pesticides (e.g., McCaffery, 1998; Chaturvedi, 2007; Yang *et al*., 2013).

Knowing seasonality, phenology and number of generations of a target pest is crucial to practice effective pest management; the knowledge tells, for example, the optimal timing and duration of pesticide application, improving the pest control strategy. The seasonality, phenology and number of generations are affected by a number of abiotic and biotic factors but ambient temperature is among the most important factors (Davidson, 1944; Ives, 1973; Tauber *et al*., 1986; Kiritani, 1997). This is because temperature is a primary determinant influencing the rate of development of insects (Wagner *et al*., 1984; Honěk and Kocourek, 1990). Temperature is also a significant factor affecting the survival and size of insects, which can directly and indirectly impact their population dynamics (Tauber *et al*., 1986; Kiritani, 2006).

Examining the effects of temperature on the survival, development and size of insect pests is thus the primary step in pest research. Many studies in fact have investigated the relationship between temperature and development of *H. armigera* (e.g., Qureshi *et al*., 1999; Jallow and Matsumura, 2001; Barteková and Praslička, 2006; Mironidis and Savopoulou–Soultani, 2008; Mironidis, 2014). Further, temperature is suggested to be one of

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the most important factors affecting the seasonality and number of generations of *H. armigera* populations (King, 1994). However, it is known that such relationships in insects are modified depending on their geographic strains to adapt the local environment (Tauber *et al.*, 1986).

Despite the fact that *H. armigera* is a key pest of agricultural crops in Vietnam, no published data are currently available on the lower developmental threshold and temperature constants for Vietnamese *H. armigera*. In addition, relatively few studies examined how temperature could affect the survival and size of *H. armigera* though a number of previous studies have addressed the effect of temperature on the development of *H. armigera*. As an aid to understanding the field phenology of *H. armigera* in Vietnam, it is necessary to clarify the heat requirements for its growth, development and survival using Vietnamese *H. armigera*. Accordingly, the present paper focuses on the effect of temperature on *H. armigera* development, growth and survival. This study also determines the lower development threshold and thermal constants for Vietnamese *H. armigera*. The information obtained in the present study will help construct phenological models for evaluation of pest management strategies and for population dynamics analysis and may also contribute to a better understanding of the effects of climate change on *H. armigera* phenology.

MATERIAL AND METHODS

General rearing procedures

Helicoverpa armiger used in our study was originated from Gia Lam, Hanoi, northern Vietnam. The laboratory colony has been maintained for generations in the laboratory using mung bean sprouts. Wild–caught individuals were frequently added to the colony to prevent inbreeding.

We followed the method of Ali *et al.* (2009); the first and second instars were reared collectively, and the third instars were held individually, in plastic containers (6 × 6 × 6 cm) until pupation to prevent cannibalism. Bean sprouts for feeding were exchanged on the daily basis. Pre–pupae were transferred into a clear container (6 × 6 × 6 cm) filled with 4cm of moisture soil for pupation. After pupation, they were sexed and transferred into a clear container lined with filter paper for adult emergence. Newly emerged adults were paired as per suggestions by Bhatt and Patel (2001) and were then reared in mating cages (50 × 50 × 50 cm) covered with a fine mesh net. The adult moths were fed on 20% honey solution. Male moths were kept in the cages for 3 days to ensure mating and then removed from the cages. The eggs oviposited were collected from the mesh net every 24h.

Effect of temperature on development and survival

We examined the effects of three different temperatures on the development and survival of *H. armigera*, by following the protocol of Barteková and Praslička (2006). Newly laid eggs were held in an incubator that was maintained at one of three different temperatures (20, 25 and 30 ± 0.5°C) with 70 ± 10% RH and a photoperiod of 12L: 12D. The eggs were observed every 24h to record larval hatching. Newly hatched larvae were transferred individually into plastic containers with a cloth lid for ventilation. 70 larvae were used for each temperature group. Fresh food, i.e., mung bean sprouts, was provided arbitrarily, and larvae were observed daily until pupation. When pupated, food provision was ceased, and pupal weights were recorded with a balancer. The pupae were checked daily for adult emergence.

The lower developmental threshold (To) and the thermal constant (K)

The developmental rates and thermal thresholds were calculated by means of linear regressions as follows (Campbell *et al.*, 1974): For each temperature group, rates of development (DR) are estimated as reciprocals of development time (DT). The relation between developmental rate (DR) and temperature (T) is described by a function (the regression line equation):

$$y = a + bx$$

where y = developmental rate, a = constant term and b = regression coefficient.

The lower developmental threshold (T_o) is determined as:

$$T_o = -a/b$$

The sum of effective temperatures (K), i.e., number of day–degrees above LDT necessary for completion of development is

$$K = 1/b$$

The thermal units required for completion of development of each stage are determined according to the equation of thermal summation (Blunk, 1923):

$$K = y\,(T - T_o)$$

where y = developmental rate, T = temperature in degree centigrade, T_o = lower threshold of development and K = thermal units (degree–days).

Data analysis

The mean development time and the number of eggs laid per female were compared among the groups with an ANOVA using Statview 5.0. Simple regression analyses were made to examine the relationships between the pupal weight and number of eggs laid per female on each group. The data of pupae that had failed to emerge were discarded.

RESULTS AND DISCUSSION

In our study, *Helicoverpa armigera* was reared on mung bean sprouts under three different temperatures. The results showed that the ambient temperature greatly affected the survival, development and growth of *H.*

armigera.

The duration of each developmental stages decreased as temperature increased from 20°C to 30°C (Table 1). The duration of the egg stage significantly differed among the 3 groups (ANOVA; F = 347.08, $P < 0.05$). Temperature also had a significant effect on the duration of the larval stage (Table 1; ANOVA; F = 1508.95, $P < 0.05$) and on the pupal stage (ANOVA; F = 872.61, $P < 0.05$). Jallow and Matsumura (2001) reported that the egg duration at 20, 25, 30°C were 5.5, 3.0 and 2.6 days, respectively while Barteková and Praslička (2006) showed 11.17, 7.0 and 4.07 days for the same temperature groups. Our data were similar to the former study but were considerably different. For larval stage, our results were rather close to Barteková and Praslička (2006) in which the larval development time were reported to be 39.3 and 14.07 days at 20 and 30°C, respectively. Also, for pupal development, similar values were recorded by allow and Matsumura (2001) and Barteková and Praslička (2006).

Further, the analysis showed that temperature influenced the survival rate of *H. armigera* larvae (Table 2). The final survival rates, i.e., from egg to adult emergence, increased with increasing temperatures (48.57%, 64.29% and 75.71% at 20°C, 25°C and 30°C, respectively), and differed significantly among the temperature groups (chi–squared test; df =2, $x^2 = 11.24$, $P = 0.0036$). In all temperature groups, the survivorships of early instar larvae and pupal stage were lower than late instar larvae; survival rates were 100% in 4th, 5th and 6th instars. In addition, temperature significantly affected pupal weights (ANOVA; F = 15.684; $P < 0.05$); larvae reared at higher temperatures were heavier at pupation (Fig. 1).

The knowledge of the thermal constants and lower development thresholds is essential information to determine the developmental ecology of arthropods. Thermal

Table 1. Life cycle of *H. armigera* under different temperatures

Stage	Period (days)		
	20°C	25°C	30°C
Egg	5.36 ± 0.06 (70)	3.44 ± 0.06 (70)	2.44 ± 0.06 (70)
1st Instar	5.33 ± 0.11 (49)	2.15 ± 0.11 (55)	1.37 ± 0.06 (59)
2nd Instar	5.56 ± 0.15 (45)	3.30 ± 0.12 (53)	2.30 ± 0.09 (57)
3rd Instar	4.67 ± 0.23 (43)	2.23 ± 0.09 (52)	1.79 ± 0.08 (57)
4th Instar	4.86 ± 0.15 (43)	2.56 ± 0.13 (52)	2.30 ± 0.10 (57)
5th Instar	6.21 ± 0.21 (43)	2.77 ± 0.11 (52)	2.02 ± 0.08 (57)
6th Instar	12.79 ± 0.23 (43)	6.08 ± 0.20 (52)	5.30 ± 0.07 (57)
Larval duration	39.21 ± 0.47 (43)	18.90 ± 0.30 (52)	15.21 ± 0.20 (57)
Pupae	18.65 ± 0.33 (34)	13.07 ± 0.15 (45)	7.23 ± 0.12 (53)
Pre–oviposition	5.83 ± 0.19 (18)	3.38 ± 0.11 (21)	2.31 ± 0.08 (32)
Total life cycle	51.78 ± 0.85 (18)	38.38 ± 0.41 (21)	26.19 ± 0.20 (32)

Note: Data are shown as mean ± SE. The means in the same rows are significantly different between the groups in each development stage ($P < 0.05$, Fisher's PLSD). Values in parentheses are number of sample size.

Table 2. Survivorship of *H. armigera* under different temperatures

Stage	Survivorship (%)		
	20°C	25°C	30°C
1st Instar	70.00 (70)	78.57 (70)	84.29 (70)
2nd Instar	91.84 (45)	96.36 (53)	96.61 (57)
3rd Instar	95.56 (43)	98.11 (52)	100.00 (57)
4th Instar	100.00(43)	100.00(52)	100.00(57)
5th Instar	100.00(43)	100.00(52)	100.00(57)
6th Instar	100.00(43)	100.00(52)	100.00(57)
Pupae	79.07 (34)	86.54 (45)	92.98 (53)
Survivorship from larva to adult (%) *			
	48.57 (70)	64.29 (70)	75.71 (70)

*Survival rates from 1st instar to adult emergence significantly differed among the temperature groups (Chi–squared test; $P = 0.0036$).

**Numbers in parentheses indicate sample size.

constants are frequently used to create predictive models of pest population dynamics in various environments (Honěk, 1996). We calculated the developmental rate, lower developmental threshold and thermal constant, and the estimated values were summarized in Table 3. The temperature influence on egg development was indicated by a regression line equation (Fig. 2; y = 0.022x – 0.26) with a high correlation coefficient (r^2 = 0.99). The line showed that the developmental rate of egg increased with increasing temperature, indicating the positive correlation between the variables. According to the regression line equation we computed the lower developmental threshold (T_o) of *H. armigera* eggs to be 11.5°C, and the thermal constant for the development of eggs (K) as 44.8 day–degrees. These results are in line with the findings of Mustapha and Matsumura (2001) on tomato and Mohammed *et al.* (1999) on Insecta LF, in which the lower developmental thresholds and the thermal constants were 10.5°C, 51 day–degrees and 10.8°C, 45.5 day–degrees, respectively.

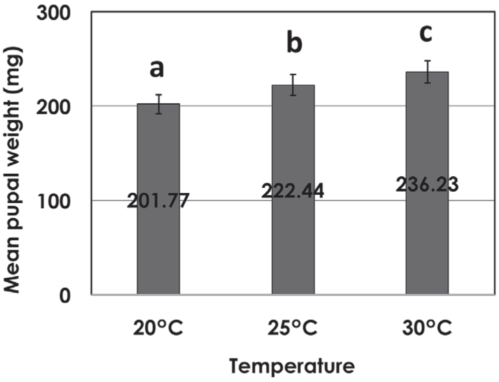

Fig. 1. Pupal weights of *H. armigera* when reared at different temperatures. The mean values differed significantly among the groups, and different letters above the bars show a significant difference (see the text).

Similarly, we obtained a regression line equation for the larval stage (Fig. 2; y = 0.0040x – 0.053; r^2 = 0.96), and the lower developmental threshold (T_o) estimated was 13.3°C, and the thermal constant 250.0 day–degrees. Mustapha and Matsumura (2001) also reported the lower developmental threshold and the thermal constant for larval stage were 11.3°C and 215.1 day–degrees, respectively. Barteková and Praslička (2006) reported that the lower developmental threshold of larval stage was 11.3°C but in contrast, the thermal constant for larval stage was 344.8 day–degrees. Thus, the values estimated in our study were slightly different from those in other studies.

For the pupal stage, a regression line equation (y = 0.0085x – 0.12; r^2 = 0.93) was obtained (Fig. 2). The lower developmental threshold (T_o) of *H. armigera* pupae was estimated as 14.4°C, and the thermal constant 117.6 day–degrees. Mohammed *et al.* (1999) obtained similar values for the lower developmental

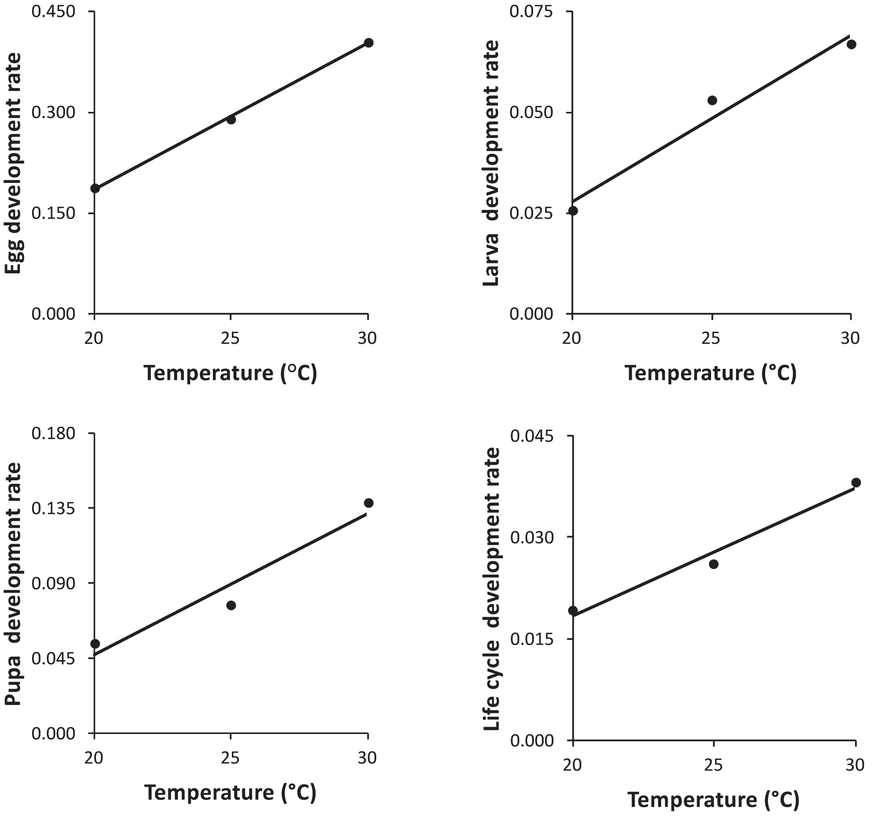

Fig. 2. Regression lines describing the relationships between temperature and developmental rate of egg, larval, pupal and life cycle (see the text in details).

threshold and thermal constant of pupal stage (14.6°C and 142.9 day–degrees, respectively). Thus, the temperature effect on life cycle period was expressed by a regression line equation (Fig. 2; $y = 0.0019x - 0.019$; $r^2 = 0.97$), and the lower developmental threshold (T_o) and thermal constant of Vietnamese *H. armigera* life cycle were 10.2°C and 526.3 day–degrees, respectively.

The present results show that temperature is an important environmental determinant affecting the survival, development and growth of *H. armigera*, suggesting also that it is an important regulatory factor of its seasonality, phonology and population dynamics. Because these should also be influenced by other factors such as weather conditions, predation, parasitism, and inter– or intraspecific competition (Fitt, 1989), field studies are necessary to examine the actual seasonality, phenology and population dynamics of *H. armigera*.

It is known that the thermal threshold and thermal constant are closely related to the adaptation of populations to the local climate (Blackman, 1987; Ikemoto, 2003). Also, the information is useful for forecasting the seasonality and phenology of insect pests (Tauber *et al.*, 1986; Kiritani, 2006). Despite the fact that *H. armigera* has been the most dangerous pests of agricultural crops that cause severe damage to corn and other crops, there are no published information on the lower developmental threshold and temperature constants for this key pest in Vietnam.

In the present study, we calculated the lower threshold temperatures for Vietnamese *H. armigera*. These values can be used in predicting potential distributional range and appearance of symptoms during the growing season because no development occurs when temperature is below that level and because insects are likely to be inactive during the months when average temperatures are below the level (Wagner *et al.*, 1984; Kiritani, 2006; but see also Mironidis, 2014 for how fluctuating temperatures lower the level).

The lower threshold temperatures estimated for Vietnamese *H. armigera* were found to be beyond 10°C regardless of its developmental stages (Table 3). In Hanoi, Vietnam, January and February are coldest winter months but the average temperatures in these months are beyond 14°C. Therefore, from our study it is theoretically predicted that *H. armigera* is likely to develop slowly during the winter months. Rates of survival and development then increase in later seasons, producing a larger number of *H. armigera*, which may ultimately invade crop fields causing economic damage. Our study thus provides implications to judge potential infestation levels in different seasons.

Thermal constants can be used to predict the number of generations per year (e.g., Fitt, 1989; Kiritani, 2006). We therefore estimated the possible number of generations of *H. armigera* in Hanoi, Vietnam on the basis of day–degree requirements and theoretical developmental zeros obtained in the present study. The total thermal units in one year for *H. armigera* was:

$Q = 31(19.06 - 10.2) + 28(20.11 - 10.2) + 31(21.74 - 10.2) + 30(24.95 - 10.2) + 31(28.63 - 10.2) + 30(31.14 - 10.2) + 31(30.26 - 10.2) + 31(30.11 - 10.2) + 30(30.28 - 10.2) + 31(27.31 - 10.2) + 30(24.23 - 10.2) + 31(17.46 - 10.2) = 5585.1$°C. The expected number of generation per year in Hanoi, Vietnam was then calculated as follows: $Q/K_{\text{life cycle}} = 5585.1/526.3 = 10.61$ generations. Thus, Vietnamese *H. armigera* may complete a maximum of 10–11 generations per year in Hanoi region.

In tropical and subtropical regions, this pest may breed continuously throughout the year, passing through more than 10 generations (Fitt, 1989). However, generations may not be clearly discrete and may hence overlap, making it difficult to separate the generations in later seasons. Taken together, *H. armigera* is expected to be seen throughout the year with up to 10–11 generations per year without clearly discrete generations in later seasons.

Our study demonstrated the survival and growth of *H. armigera* is negatively affected by lower temperatures even when the temperature range is between 20°C and 30°C (Table 2). Several abiotic and biotic factors have been so far identified to influence the survival of *H. armigera*. For example, the larval survival differs greatly among host plants (e.g., Casimero *et al.*, 2000; Jallow *et al.*, 2001; Naseri *et al.*, 2011; Reigada *et al.*, 2016). Extreme temperature conditions also have a negative effect on *H. armigera* (Mironidis and Savopoulou–Soultani, 2008). It is also known that winter temperatures during the diapausing stage greatly impact the survival of lepidopterans (Tran *et al.*, 2007; Morey *et al.*, 2012) and this holds true for *H. armigera* (Huang, 2016). In addition, high temperature conditions like 35°C was shown to be harmful for the development (Mironidis and Savopoulou–Soultani, 2008).

Few previous studies have given evidence that *H. armigera* survival and growth are dependent on ambient temperatures within a rather favorable range, and these are lowered even at 20°C condition. The present study suggests that Vietnamese *H. armigera* popula-

Table 3. Influence of temperature on *H. armigera* development

Stage	Development rate			Regression equation	R^2	T_o	K
	20°C	25°C	30°C				
Egg	0.187	0.291	0.410	$y = 0.0223x - 0.2625$	0.9985	11.5	44.8
Larva	0.026	0.053	0.066	$y = 0.0040x - 0.0526$	0.9581	13.3	250.0
Pupa	0.054	0.077	0.138	$y = 0.0085x - 0.1223$	0.9343	14.4	117.6
Life cycle	0.019	0.026	0.038	$y = 0.0019x - 0.0193$	0.9736	10.2	526.3

tions show local adaptation, favoring warmer regions like Vietnam.

Developmental duration, the lower developmental thresholds and thermal constants estimated in our study are slightly different from those previously reported. Some previous studies used artificial diets for rearing the moth larvae. The difference may be due to the fact that the development of *H. armigera* is faster on artificial, nutritionally superior food (Jallow *et al.*, 2001). Development, growth and survival of *H. armigera* may also be variable depending on host plants (e.g., Jallow *et al.*, 2001; Naseri *et al.*, 2011; Reigada *et al.*, 2016). Further, it is well established that life history parameters including thermal constant and lower developmental threshold can differ among geographic strains of insects because of local adaptation. In fact, induction, duration and termination of diapause are reported to depend on geographic populations of *H. armigera* in China (Chen *et al.*, 2013a, b). Thus, careful experimentation is needed to assess how the interactions among temperature, host plants and geographic strains could affect *H. armigera* development, growth and survival for a better prediction. This will be investigated in a separate study.

The mean pupal weights calculated in our study are between 202 and 236 mg (Fig. 2). The values are smaller than those reported in previous studies (Casimero *et al.*, 2000; Jallow *et al.*, 2001). Because nutritional quality can affect the size of *H. armigera* and other lepidopterans, (Casimero *et al.*, Jallow *et al.*, 2001), smaller *H. armigera* obtained in the present study may be due to a low nutritional value of bean sprouts used in our study. Curiously, previous studies reporting the survival rates of *H. armigera* demonstrated lower rates of larval survival around 40–60% at 25°C in most of host plants examined (Jallow *et al.*, 2000) whereas the larval survival rate was 74.3% in our study. Further, the survival was even higher at 30°C, and is 81.4%. If bean sprouts should not be nutritionally optimal, then the high survival rates observed in our study could be explained by a lack of plant defensive chemicals, which would be rather accumulated in the latter growth stage of plants.

In Vietnam, the main current measure to control *H. armiger* is chemical control. However, IPM practices incorporating other measures would be required due to resistance and resurgence. There are several measures suggested to implement (Fitt, 1989). In Vietnam, there are many lepidopteran pests that are difficult to control solely by chemical pesticides. Therefore, combination of other control measures, such as conservation of natural enemies, use of pheromone traps and resistant varieties, have been suggested and tested for effective management of such pests (e.g., Ueno, 2006, 2015a, b; Ho *et al.*, 2013, 2014; Tran *et al.*, 2016, 2017). These measures may also be applicable to *H. armiger* management. In any case, ecological and regional understandings of *H. armiger* are essential to practice effective management of Vitnamese *H. armigera*, and the present study provides useful information for this purpose.

Author contributions

T. T. G. Ho designed the present study. H. G. Trinh and H. Virachack conducted most of the experiments. T. Ueno and T. T. G. Ho interpreted the data and prepared the manuscript. All authors approved the final version of the manuscript.

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