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Effects of Larval Rearing Temperature and Host Plant Condition on the Development, Survival, and Coloration of African Armyworm, *Spodoptera exempta* Walker (Lepidoptera: Noctuidae)

ABSTRACT

Effects of temperature and host plant condition on insect development have been examined in a number of studies but their combined effect is not well investigated. In this study the effects of varying temperatures and host plant conditions and its interaction on development, survival, and coloration of solitarious and gregarious forms of African armyworm (AW), Spodoptera exempta, an outbreak pest species, were studied under laboratory condition. Rearing temperature was found to have significant effects on larval and pupal development and pupal weight in both solitarious and gregarious forms. The effects of host plant condition in both forms were variable; significant effects were consistently observed in pupal development for both gregarious and solitarious forms but not in larval development and pupal weight. Larval and pupal survival of the solitarious form significantly decreased with the decreased in temperature, while only pupal survival decreased with the decreased in temperature in gregarious form. Distinct larval coloration was also observed in different temperatures. Larvae reared at high temperature exhibited lighter coloration, while larvae reared at low temperature exhibited darker coloration regardless of rearing density. The significant interaction of temperature and host plant condition on many aspects of insect fitness measured in this study highlights the need for further studies on the effects of other environmental factors such as relative humidity, rainfall, and light intensity to improve predictions as to how these insect pests will respond to climate change.

Key words: *Spodoptera exempta, Noctuidae, African armyworm, rearing temperature, host plant condition*

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INTRODUCTION

The African armyworm, *Spodoptera exempta*, is an important pest of pasture and cereal crops in Africa, Arabian Peninsula, Australasia, Oceania, and Southeast Asia (*CABI 2007*). In the Philippines, its larvae voraciously feed on young stages of cereal crops like corn, rice, sugarcane, wheat, and all types of grasses (*Gabriel 1975*). *S. exempta* is a pest with outbreak occurrence. It is migratory in nature, and the location, timing, and magnitude of its outbreaks are difficult to predict. Marked seasonal occurrences of outbreaks of *S. exempta* have been reported in different areas of the world particularly in Africa (*Brown 1962*). The cause of these outbreaks centers mainly on climatic factors, operating directly or indirectly through their effect on vegetation. Rainfall, together with availability of food source (i.e. young succulent leaves), enables *S. exempta* to persist and produce successive generations in the field (*Khasimuddin and Lubega 1979*). Most of the outbreaks of the species have been reported to occur during the rainy season especially after periods of prolonged drought (*Brown 1962*; *Tucker 1983*; *Haggis 1986*). *Hattingh* (*1941*) noted that the fitness of *S. exempta* is strongly influenced by temperature. In the Philippines, outbreak of *S. exempta* occurred in several places immediately after a long dry season (December 2009-June 2010), which caused localized damage to sugarcane, rice, corn, and pasture grasses.

Larva of *S. exempta* exhibits a density-dependent phase polyphenism, which has "solitarious" and "gregarious" forms. The gregarious forms are found in dense outbreaks, while the solitarious forms are rarely found in the field and are usually in low densities. The phase change in *S. exempta* is a stress phenomenon associated with crowding. The role of polyphenism in the ecology of the species and its importance in the development of outbreak has remained a matter of debate and is still unknown due to the lack of field data on the solitarious phase, which is rarely visible in the field (*Gunn 1998*).

In general, developmental rate of *S. exempta* is affected by various factors such as temperature, larval density, and food-plant type and quality. Most experiments done concentrated on direct effect of temperature on some life history traits of *S. exempta* (*Brown 1962*). In nature, however, temperature can also affect insects indirectly through its direct effect on host plants. Host plants under extreme temperature could be water-stressed, presenting poor nutritional supply to larvae. This study was conducted to help shed light on the effect of larval rearing temperature and host plant condition on development, growth, and survival of *S. exempta*. Specifically, it aims to: determine the effects of temperature on host plant conditions (i.e. well-watered and water-stressed), on the larval and pupal development and coloration of gregarious and solitarious forms of *S. exempta*; and quantify the survival of the larval instars and pupa of *S. exempta* reared under varying temperatures and host plant conditions.

MATERIALS AND METHODS

Study insect. An initial single population for the laboratory stock cultures of *S. exempta* was collected in Sariaya, Quezon (13.9670°N, 121.5330°E) in the Southern part of the Philippines during the outbreak in August 2010. It was chosen because it was the nearest site with confirmed reported outbreak during that time. A total of 120 larvae were reared singly (n = 40) and in groups (n = 80; 10-15 per container) in plastic containers (24±2°C) using young corn leaves *ad lib* until pupation. Pupae were placed in 10 cages for adult emergence. Sugar solution (50%) in cotton was used to feed adults. Fresh sweet potato tops were provided as oviposition substrate. Egg masses were collected and kept in acrylic pans until hatching. Larvae from the same cohort were used in each of the experimental set-ups.

Experimental Treatments

Host plant. Philippine Super Sweet No. 1 or *asukar* was the corn variety used for rearing stock cultures and in all treatments. Two to three plants were grown in each plastic pot (250 ml) containing a mixture of coir dust and garden soil. Young seedlings were regularly watered for 13 days after germination. Each pot was watered with tap water until the soil was more or less saturated. After this period, they were divided into two groups; water-stressed (WS) plants (i.e. watered once a week) and well-watered (WW) plants (i.e. watered daily). Using oven dry weight (ODW) as basis, the moisture content (MC) of WS plants was determined at 60-70% while that of WW plants was determined at 80-90%. Moisture content of WW plants was within the range of reported optimum condition for common agricultural crops.

Effect of temperature and host plant conditions on development and survival. The effects of temperature and host plant conditions on development and survival of S. exempta were studied under laboratory conditions. The treatments were arranged in a 2x3 Factorial Complete Randomized Design (CRD). Three temperature regimes and two host plant conditions were used in the study; high temperature (34±2°C), room temperature (28±2°C), and low temperature (22±2°C) and water-stressed (WS) and well-watered (WW) plants, respectively. Room temperature and well-watered plants were considered as the control. Whorls of two-week old corn seedlings were artificially infested with newly-hatched larvae of the same cohort. Gregarious forms were maintained at a density of 10-15 per plant in 3-4 replicates while solitarious forms were maintained at a density of 1-2 per plant in 10 replicates. Plants were covered with 20 x 13 cm nylon mesh sleeve cage and were transferred to temperature-controlled rooms and chambers. High temperature was manipulated by controlling the lighting of six 50 watts yellow incandescent bulb to attain the desired temperature. Low temperature regime was set in an air-conditioned laboratory room. Room temperature was manipulated by placing the set up in a non-ventilated laboratory room. Temperature in each regime was monitored every three hours during the day. Larvae were reared until pupation. Larval duration and instar survival were recorded. Collected pupae were individually kept in net-covered 250 ml plastic cups containing sandy loam soil. Pupae were weighed using an analytical balance after 48 hours from collection. Weights were converted to milligrams as indicated in **Table 1**. Pupae were exposed to the same temperature gradients as the larvae. Pupal duration and survival was recorded. Changes in larval coloration were also observed.

Data analysis. One-way analysis of variance (ANOVA) was used to determine the differences in development time and pupal weight. The survival data was analyzed through Approximate Z-test (5% and 10% levels of significance). Treatment means were compared using Scheffe's test. All tests were done using Statistical Analysis Software (SAS 9.0).

RESULTS

Effects of temperature and host plant condition on development of *S. exempta*. Temperature and host plant conditions significantly affected the development of *S. exempta* (**Table 1**). The development time of larvae and pupae of *S. exempta* varied significantly with temperature regardless of host plant conditions. It was significantly shortened with increased temperature and was generally longer in solitarious than in gregarious forms (**Table 2**). In addition, temperature had evident effects in the duration of each larval instar as well as in the number of instars the larvae underwent. Development of each instar was generally shortened as the temperature was increased. Solitarious larvae reared in room temperature and in high temperature underwent five larval instars, while those reared in low temperature had six larval instars. On the other hand, gregarious larvae reared in three temperatures all underwent six larval instars regardless of host plant condition. Pupal weight, on the other hand, was significantly affected by larval feeding on low quality host plants. Pupal weights were lower in larvae fed with water stressed plants than with well watered plants.

Analysis of variance (one-way ANOVA) on the effects of temperature, host plant condition, and their interaction showed the importance of larval rearing temperature and host plant conditions on the development of the solitariousand gregarious forms of *S. exempta* (**Table 2**). In both forms,

Table 1. Effects of varying temperatures and host plant conditions on development time and pupal weight of solitarious and gregarious forms of *S. exempta*.

Trait	Host Plant Condition	T°C	Phase	
			Solitarious	Gregarious
Development Time (days)				
Larval stage	Well-watered	34±2	10.45± 0.22[b]	9.50 ±0.29[b]
		28±2	13.81± 0.57[b]	15.30 ±0.78[b]
		22±2	27.10± 0.96[a]	18.50 ±0.49[a]
	Water-stressed	34±2	11.00± 0.63[b]	10.20 ±0.26[b]
		28±2	12.47± 0.38[b]	13.00 ±1.07[b]
		22±2	29.70± 0.89[a]	19.30 ±0.71[a]
Pupal stage	Well-watered	34±2	7.81± 0.21[d]	6.00 ±0.38[c]
		28±2	11.40± 0.21[c]	10.70 ±0.37[b]
		22±2	20.00± 0.86[a]	16.20 ±0.39[a]
	Water-stressed	34±2	8.00± 0.26[d]	6.40 ±0.24[c]
		28±2	11.44± 0.17[c]	11.30 ±0.18[b]
		22±2	18.20± 0.16[b]	17.50 ±0.31[a]
Pupal Weight (mg)	Well-watered	34±2	142.00±5.22[a]	131.00 ±2.97[d]
		28±2	118.00±6.74[b]	107.00 ±8.55[c]
		22±2	100.00±8.15[c]	155.00 ±3.31[a]
	Water-stressed	34±2	107.00±6.31[a]	137.00 ±5.38[cd]
		28±2	95.00±5.27[b]	82.00 ±7.02[b]
		22±2	111.00±10.66[a]	128.00 ±5.51[cd]

Means within columns followed by same letters are not significantly different at $P < 0.05$.

the effects of rearing temperature on both larval and pupal development and pupal weight were consistently highly significant ($P < 0.001$). In solitarious form, the host plant condition had significant effects on pupal development and weight, while in gregarious form, the host plant condition had significant effects on larval and pupal development but not on pupal weight. In solitarious forms, the interaction of temperature and host plant condition had significant effect on larval and pupal development and pupal weight while in gregarious form, interaction between temperature and host plant conditions had significant effects only on larval development and pupal weight.

Effects of temperature and host plant condition on survival of *S. exempta*. Larval and pupal survival in the well watered plants was affected by varying temperature (**Table 3**). In the solitarious form, the larval and pupal survival both significantly decreased with decreased temperature. In the gregarious form, the pupal survival significantly decreased as the temperature was decreased. In addition, the cumulative percent mortality of both forms of S. exempta generally increased as larvae reach later instars regardless of temperature and host plants conditions (**Figure 1**). As expected, mortality of larvae reared in room temperature (28±2°C) is generally higher and occurred earlier in larvae fed with water-stressed plants.

Effect of temperature and host plant condition on larval coloration of *S. exempta*. Larvae reared in isolation began to show distinct features of the solitarious phase in the third or fourth instar as expected. Their color varied from light green, pale pink, gray, and brown to black. All larvae exhibited the typical solitarious form having green body with a brown dorsal stripe at the center. Most of the solitarious larvae reared in high temperature (34±2°C) had light olive green or lighter melanisation, while those reared in low temperatures (22±2°C) had generally darker cuticular melanisation (**Figure 2**).

Larvae reared in groups showed the typical black to dark green appearance during the gregarious phase in the third or fourth instar molt when reared at room and low temperatures. Most of the gregarious larvae reared at high temperatures had light olive green similar to the solitarious phase. Gregarious larvae reared in low temperatures had maroon to black cuticle and were much darker compared to the larvae reared in room and high temperatures (**Figure 3**).

DISCUSSION

Development was generally shortened with increased temperatures. These results are parallel to other studies on S. exempta (*David et al. 1975*; *Jansenn 1994*; *Persson 1981*; *Simmonds and Blaney 1986*). The duration of the larval and pupal stage of the gregarious forms reared in corn at various temperatures observed in this study is within the range of reported duration of the larval stage by previous studies (*Rimando 1954*; *Simmonds*

Table 2. Analysis of variance (one-way ANOVA) of development time and pupal weight of solitarious and gregarious *S. exempta* as affected by temperature (T), host plant condition (H) and their interaction (T x H).

Trait	Effect	DF	*F*-Value	*P*-Value
Solitarious				
Length of Larval Development	T	2	444.83	< 0.0001***
	H	1	1.77	0.1869ns
	T x H	2	4.94	0.0093**
Length of Pupal Development	T	2	649.82	< 0.0001***
	H	1	4.81	0.0317*
	T x H	2	5.82	0.0046**
Pupal Weight	T	2	5.39	0.0063**
	H	1	7.45	0.0077**
	T x H	2	4.95	0.0093**
Gregarious				
Length of Larval Development	T	2	183.50	< 0.0001***
	H	1	0.27	0.0023**
	T x H	2	3.52	0.0060**
Length of Pupal Development	T	2	451.54	< 0.0001***
	H	1	6.96	0.0116*
	T x H	2	0.93	0.4007ns
Pupal Weight	T	2	186.41	< 0.0001***
	H	1	0.15	0.6984ns
	T x H	2	3.76	0.0266**

* Significant at P < 0.05,** Significant at P < 0.01,*** Significant at P < 0.10, ns-not significant

Table 3. Effect of varying temperatures and host plant condition in larval and pupal survival of solitarious and gregarious forms of *S. exempta*.

Trait	Host Plant Condition	T°C	Phase	
			Solitarious	Gregarious
Larval Survival (%)				
	Well-watered	34±2	73.00a	61.00a
		28±2	80.00a	83.00a
		22±2	41.00b	64.00a
	Water-stressed	34±2	59.00a	67.00a
		28±2	75.00a	45.00b
		22±2	63.00a	56.00a
Pupal Survival (%)				
	Well-watered	34±2	84.00b	100.00a
		28±2	83.00b	90.00a
		22±2	50.00c	79.00b
	Water-stressed	34±2	59.00c	71.00b
		28±2	100.00a	88.00a
		22±2	69.00b	59.00b

Means within columns followed by same letters are not significantly different at P < 0.05 (Scheffe's Test)

and Blaney 1986; *Yarro 1984*; *Cheke 1995*). Temperature has been identified as the main factor directly affecting herbivorous insects and can have profound influence on their development, survival, and abundance. The effect of elevatedtemperature is known to alter the phytochemistry of the host plants and affect the insect growth and development directly or indirectly through effect on host plants (*Rao 2006*).

Larval development was delayed on water-stressed host plants. Pupal weight was low with larvae fed with low quality host plants. Insect herbivores growth and development are often intimately linked to host plant quality (*Bernays 1990*). Several studies have shown that larvae fed with unbalanced diets (i.e. stressed host plants) generally exhibit lower survival, delayed larval development, and lower pupal mass (*Despland and Noseworthy 2006*; *Lee et al. 2002*; *Liu et al. 2004*).

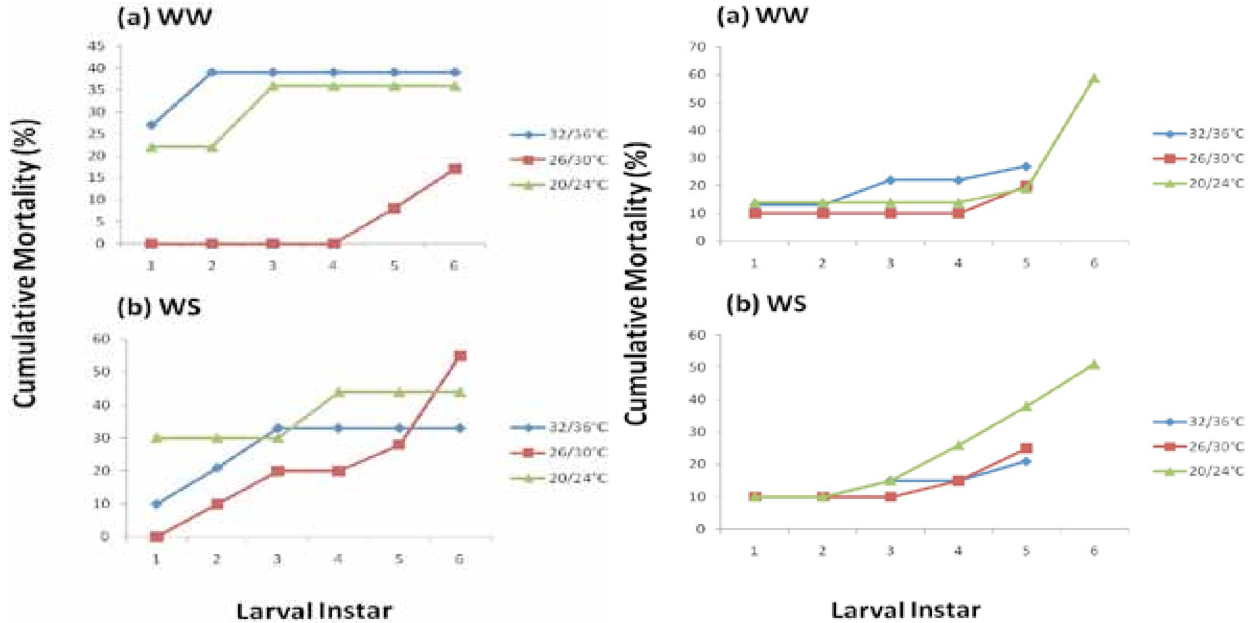

Figure 1. Cumulative mortality of *S. exempta* solitarious larvae (left) and gregarious larvae (right) reared under different temperatures and host conditions.

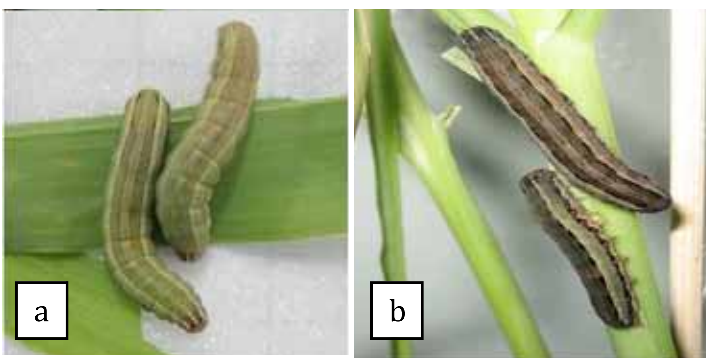

Figure 2. Solitarious larvae of *S. exempta* reared at a) high and b) low temperatures.

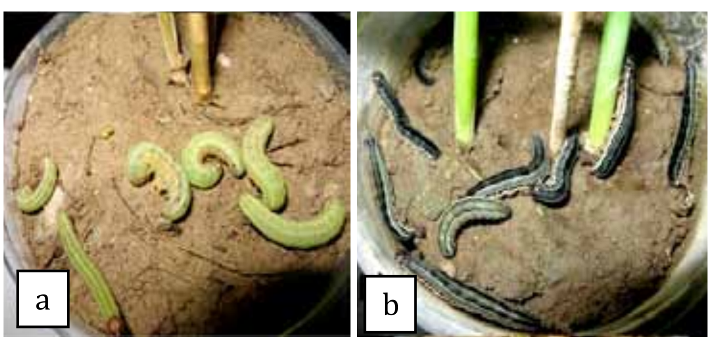

Figure 3. Gregarious larvae of *S. exempta* reared at a) high and b) low temperatures.

Survival of solitarious and gregarious forms of *S. exempta* varied among different temperature regimes and host plant conditions. With this finding, we can posit two hypotheses that can help explain the occurrence of *S. exempta* outbreaks; the differential survival and form-shift (*L.R.I. Velasco pers. comm.*). In the differential survival, solitarious larvae tend to survive at high temperature while gregarious larvae at low temperature. This tendency was observed during the occurrence of *S. exempta* outbreak on the first two months after the start of the short rainy season. Based on observations, population of solitarious larvae, which is the natural form of the insect, tends to decline with cooler temperature. This becomes an opportunity for the population of the gregarious form to increase. On the other hand, in the form-shift, the solitarious forms shift to gregarious forms during periods of drought when the temperature is high and host plants are stressed, making the resources limited in the field.

In addition, it was observed that low temperature is detrimental to pupal stage and became more prone to various pathogenic infections as evident from the growth of molds on the pupa. Low temperatures, excessive rainfall, prolonged drought, stressed host plants, and virus infection are the important mortality agents of *S. exempta* in the field (*Persson 1981*).

Based on theory, the change in cuticular melanisation is presumed to be principally determined by larval contact. In the case of the *S. exempta* the change in cuticular melanisation may be also due to change in temperature. The cuticular melanisation in both solitarious and gregarious larvae was reduced at high rearing temperatures and enhanced at low rearing temperatures. This result suggests that dramatic phase-associated change in color is not only due to density-related factors in line with the frequency of larval contact but also due to temperature. *Gunn* (*1998*) similarly observed this temperature-driven color change in the insect and attributed the color change to thermoregulation. The dark coloration of gregarious larvae was associated with its thermoconforming strategy (*Klok and Chown 1998*). Furthermore, heavy pigmentation of the gregarious forms constitutes adaptations for accelerating larval development by elevating body temperatures (*Woodrow et al. 1987*). It was suggested that the natural form of larvae for the species is the solitary type because exogenous factors (environmental and density-related) probably brings about a physiological shift to the gregarious type leading to outbreaks (*Khasimuddin 1981*). Based on our observation, gregarious forms occur in rainy seasons characterized by cooler temperatures (outbreak season) where they utilize abundant food resources.

CONCLUSION AND RECOMMENDATIONS

Temperature had significant effects on the development and survival of *S. exempta* than host plant condition. High temperature hastened the development period of both larva and pupa while low temperature reduced their survival. Host condition mainly influenced the development time and weight of pupa in both solitarious and gregarious forms. Developmental time was prolonged in water stressed plants. Pupal weights were reduced significantly in water-stressed plants. Survival varied among temperatures or host plant quality.

The significant interaction of temperature and host condition for some aspects of insect biology measured in this study highlights the need for further multifactorial studies to improve predictions as to how insect pests will respond to future climate change. Therefore, it is suggested that other aspects of insect fitness such as reproductive potential of adults should be measured to further emphasize the importance of temperature and host condition in the biology of *S. exempta*. Furthermore, it is recommended that other environmental factors such as relative humidity, rainfall, light intensity and other host plants (i. e. sugarcane and other pasture grasses) be investigated in order to fully evaluate their effects on the insect's biology. The present study has provided information fundamental to the development of new models to simulate and predict population dynamics of S. exempta especially in the midst of climate change. Hence, knowledge on insect ecology, behavior, and pest management are important in terms of the response of insects to changing climate particularly invasive insect species.

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