Temperature and relative humidity mediated life processes of *Spodoptera* species (Lepidoptera: Noctuidae)

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Abstract

Anthropogenic-mediated climate change is expected to negatively affect pest management in agriculture. Hence, we investigated the oviposition, immature mortality, and developmental processes of *Spodoptera* species (*Spodoptera exigua* (Hübner) and *Spodoptera litura* (Fabricius)) under different temperatures (20, 25, and 30°C) and relative humidity (RH) (30–35, 50–55, 70–75, and 90–95%) conditions. For fecundity, mouths of each *Spodoptera* species were released into a rectangular box whose inner walls were covered with a sheet of white paper for each combination of temperature and RH. The mouths were kept inside the box to deposit eggs for 72 h. Temperature and RH significantly affected the fecundity, with the maximum number of eggs laid in 70–75% at 30°C. The highest egg and larval mortalities were recorded in 30–35 and 90–95% RH, respectively. Temperature and RH greatly affected the developmental period (egg–adult) and adult emergence rate. The rapid development was recorded in 70–75% RH at 30°C. Higher number of adults was found with an increase in temperature and RH. Adult longevity was significantly higher in 70–75% RH at 20°C. Based on the present study's findings, temperature and RH had an individual apparent effect on the developmental processes of *Spodoptera* species instead of an interactive effect. Therefore, there is need for an in-depth study of the influence of several climatic factors, including CO_2, on the developmental modality and demographic changes of *Spodoptera* species to assess the impacts of climatic components and the sustainable development of management strategies.

Introduction

Two *Spodoptera* species (Lepidoptera: Noctuidae), the beet armyworm (*Spodoptera exigua*) and the tobacco cutworm (*Spodoptera litura*), are economic polyphagous pests that damage a wide range of field crops, vegetables, and ornamental plants in temperate and sub-tropical regions of Asia, Australasia, and the Pacific islands (Zheng *et al.*, 2011; EPPO, 2013). *Spodoptera* species are a cosmopolitan species that feed on numerous plant species, from several families of plants (Luo and Cao, 2000; Greenberg *et al.*, 2001; Xue *et al.*, 2010).

Spodoptera species generally have several instars of larvae (Ali and Gaylor, 1992); starting from the fourth instar, larvae start to cause significant damage by consuming plants (Dhir *et al.*, 1992; Sharma *et al.*, 2014; Dai *et al.*, 2017). Thus, plant damage from larvae is the most serious problem due to their heavy feeding tendency and insecticide-resistance development (Brewer and Trumble, 1991; Ali and Gaylor, 1992). Conventional insecticides are normally applied to mitigate the problem given by *Spodoptera* species. However, management of these pests has failed due to its rapidity in developing resistance to conventional chemical insecticides and its wide host range, higher mobility, and higher reproduction capacity (Brewer and Trumble, 1991; Ali and Gaylor, 1992), and a reduction in the haphazard use of broad-spectrum insecticides due to the substantial environmental concerns involved (Mascarenhas *et al.*, 1998; Osorio *et al.*, 2008; Ahmad and Arif, 2010; Lai and Su, 2011). In Korea, *Spodoptera* species are widespread in almost all provinces and cause significant damage to various field crops and vegetables (Kim and Shin, 1987; Jung *et al.*, 2019). Further, there is a significant threat of a potential distribution expansion of *Spodoptera* species on the Korean peninsula, as the species is found in a hot spot for climate change, especially global warming (Jung *et al.*, 2019). The most foreseeable impacts of climate change, in particular, will have a profound effect on herbivore insect behaviour and population dynamics (Hunter, 2001). The severity of damage caused by any pest species depends on the rate of population increase for that species, which is influenced by temperature, humidity, and

nutritional quality of the host species (Howe, 1965; Tshiala et al., 2012). It has been reported that the oviposition and development of *Spodoptera* species can be influenced by the physical/chemical attributes of the hosts as well as abiotic factors (temperature, humidity, and light) (Bae et al., 1997; Bae, 1999; Saeed et al., 2010; Maharjan et al., 2022; Maharjan et al., 2023). Several studies have been conducted on different species of *Spodoptera* addressing the effects of temperature (Fand et al., 2015; Dai et al., 2017; Maharjan et al., 2022, 2023). Majority of developmental the studies of *Spodoptera* species have done at a single RH level. Research on the combined effects of temperature and RH on life variables of *Spodoptera* species is scarce. Thus, we conducted this study to investigate the interactive effect of the temperature and RH conditions on oviposition, egg and larval mortality, development, adult emergence, and adult longevity of *S. exigua* and *S. litura* based on an artificial diet (Goh et al., 1990).

Materials and methods

Laboratory insect-rearing colony

To maintain test insect colony, *Spodoptera* species were gathered from a soybean field at the Department of Southern Area Crop Science, NICS, RDA, Miryang, South Gyeongnam Province; 35°49′40″N, 128°74′01″E, Republic of Korea in 2020. Field larval populations were raised on an artificial medium (Goh et al., 1990). Fresh mouths of each species were placed in different acryl cages ($40L \times 40W \times 40H$ cm³, with side ventilation). Inside cage, soybean plants planted in the plastic house were provided for oviposition, and a solution of honey (10%) and water were provided as a food source. Rearing cages were placed under the room conditions (26 ± 1°C, 60 ± 5% RH, and a 16:8 h L:D photoperiod). Moreover, the test insects (*Spodoptera* species) used in this experiment were originally collected from a soybean field, and reared on an artificial medium for successive generations (approx. >5 generations) under the room conditions.

Experimental procedure

One pair of each *Spodoptera* species (sex was determined based on their morphology) (EPPO, 2015; Bandoly and Steppuhn, 2016) collected from the laboratory-rearing colony was released into a rectangular box ($7L \times 7W \times 9.5H$ cm³, with topside ventilation) whose inner walls were covered with a sheet of white paper with food sources. Then, the rectangular box with adults was placed inside humidity chambers ($27L \times 20W \times 17H$ cm³) set at one of the four different relative humidity (RH) levels (30–35, 50–55, 70–75, and 90–95%) (Winston and Bates, 1960). Different salt compositions of $MgCl_2$, $Mg(NO_3)_2 \cdot 6H_2O$, NaCl, and K_2SO_4 (Duksan Pure Chemicals, Ansan-si, Gyeonggi Province, Republic of Korea) were employed for maintaining 30–35, 50–55, 70–75, and 90–95% RH levels, respectively. Each RH-maintained chamber was then placed inside incubators (Eyela, model MTI-202B, Tokyo, Japan), and temperatures were fixed at 20, 25, and 30°C, and a 16:8 h L:D photoperiod. To measure the actual temperature and RH within the humidity chambers, a HOBO data logger (Huato Log-USB, Huato Electronic Co., Ltd, Shenzhen, China) was used. To measure fecundity, mouths were kept inside the cage for 72 h, then adult *Spodoptera* species were removed from the humidity chamber, and the eggs laid on the sheet of white paper were counted. Once eggs were hatched, new larvae were transferred into individual Petri dishes (5 cm dia. × 1.5 cm height, with topside ventilation) (SPL Lifesciences Co. Ltd, Gyeonggi Province, Republic of Korea) individually and fed an artificial diet. Then, the Petri dishes were wrapped with para-film, and placed inside the same temperature and RH chamber for recording the life variables of the *Spodoptera* species. The developmental periods from egg to adult emergence were measured, and the percentage of mouth emerged was estimated according to the overall emerged mouths from the entire number of eggs laid. Seven sets of female and male mouths were utilised for each combination of temperature and RH, and the experiment was replicated ten times for each temperature and RH condition. Once mouths developed, longevity of mouths was measured by keeping each mouth separately in Petri dishes (5 cm dia. × 1.5 cm height, with topside ventilation) (SPL Lifesciences Co. Ltd, Gyeonggi Province, Republic of Korea) at the corresponding temperatures and RH with 10% honey and water solution.

Statistical analysis

Considering temperature and RH as core factors, a two-way analysis of variance (ANOVA) was performed for analysing the life variables (number of eggs laid, egg mortality, larval mortality, developmental period, mouth emergence, and longevity). Tukey's test was applied as a post-hoc analysis at the $P < 0.05$ level of significance for the effect of temperature and RH, and its interaction (PROC GLM; SAS Institute Inc., 2002).

Results

Fecundity

For *S. exigua*, mouth fecundity was varied with temperature and RH (model, $P < 0.0001$). Temperature ($P < 0.0001$) and RH ($P < 0.0001$) significantly impacted the mouth fecundity. Similarly, combined effects of temperature and RH were also significant ($P = 0.0017$). Fecundity increased with an increase in temperature. The highest fecundity 402.73 (±29.9 SE) was at 30°C and 70–75% RH (fig. 1A).

For *S. litura*, mouth fecundity was varied with temperature and RH (model, $P < 0.0001$). Temperature ($P < 0.0001$) and RH ($P < 0.0001$) significantly impacted the mouth fecundity. Combined effects of temperature and RH were also significant ($P = 0.0017$). Fecundity increased with an increase in temperature. The highest fecundity 438.97 (±11.8 SE) was at 30°C and 70–75% RH (fig. 1B).

Egg mortality

For *S. exigua*, the percentage of egg mortality was varied with temperature and RH (model, $P < 0.0001$). Temperature ($P < 0.0001$) and RH ($P < 0.0001$) significantly impacted on the egg mortality. Combined effects of temperature and RH were also significant ($P = 0.0400$). Egg mortality increased with decreasing temperature. The highest number of eggs that died was 61.91% (±5.8 SE) at 20°C and 30–35% RH (table 1).

For *S. litura*, the percentage of egg mortality was varied with temperature and RH (model, $P < 0.0001$). Temperature ($P < 0.0001$) and RH ($P < 0.0001$) significantly impacted the egg morality. However, combined effects of temperature and RH were not significant ($P = 0.1262$). Egg mortality increased with decreasing temperature. The highest number of eggs that died was 58.10% (±5.8 SE) at 20°C and 30–35% RH (table 2).
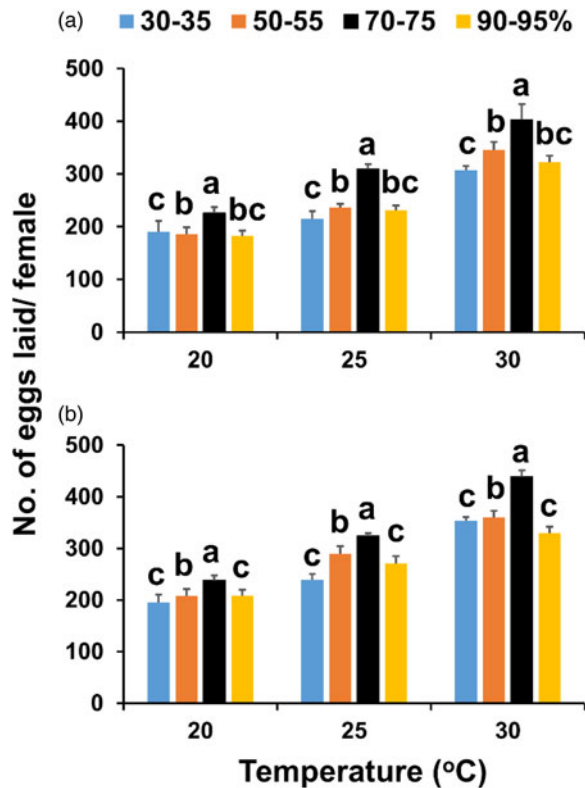
Figure 1. Temperature (20, 25, and 30°C) and relative humidity (30–35, 50–55, 70–75, and 90–95%) mediated fecundity of *S. exigua* (A) and *S. litura* (B) fed on an artificial diet over a period of 72 h. Bars represent standard error. ANOVA for *S. exigua*: model: $F_{11, 348}$ = 84.75, $P < 0.0001$, temperature: $F_{2, 348}$ = 369.55, $P < 0.0001$, RH: $F_{3, 348}$ = 57.16, $P < 0.0001$, and interaction: $F_{6, 348}$ = 3.62, $P = 0.0017$. For *S. litura*: model: $F_{11, 348}$ = 138.49, $P < 0.0001$, temperature: $F_{2, 348}$ = 619.04, $P < 0.0001$, RH: $F_{3, 348}$ = 76.05, $P < 0.0001$, and interaction: $F_{6, 348}$ = 9.52, $P = 0.0017$. Means followed by the same letters are not significantly different among relative humidity levels (ANOVA, Tukey's [HSD] test, $P < 0.05$).

Larval mortality

For *S. exigua*, the percentage of larval mortality was varied with temperature and RH (model, $P < 0.0001$). RH ($P < 0.0001$) significantly impacted the larval mortality. However, temperature ($P = 0.1122$) and the combined effects of temperature and RH did not significantly impacted the larval mortality ($P = 0.3453$). The highest percentage of larvae that died was 60.13% (± 6.9 SE) at 30°C and 90–95% RH (table 1).

For *S. litura*, the percentage of larval mortality was varied with temperature and RH (model, $P < 0.0001$). RH ($P < 0.0001$) and interactions between temperature and RH significantly impacted the larval mortality ($P = 0.0026$). However, temperature did not significantly impacted the larval morality ($P = 0.5036$). The highest number of larvae that died was 53.46% (± 10.7 SE) at 30°C and 90–95% RH (table 2).

Developmental period

For *S. exigua*, the developmental period of adult mouths varied with temperature and RH (model, $P < 0.0001$). Temperature ($P < 0.0001$) and RH ($P < 0.0001$) significantly impacted the developmental period of mouths. Similarly, the combined effects of temperature and RH were also significant ($P < 0.0001$). Developmental period decreased with increasing temperature and RH. The developmental period was shortest (16.49 days ± 0.2 SE) at 30°C and 70–75% RH (table 1).

For *S. litura*, the developmental period of adult mouths varied with temperature and RH (model, $P < 0.0001$). Temperature ($P < 0.0001$) and RH ($P < 0.0001$) significantly impacted the developmental period of mouths. Similarly, the combined effects of temperature and RH were also significant ($P < 0.0001$). Developmental period decreased with increasing temperature and RH. The developmental period was shortest (25.60 days ± 0.4 SE) at 30°C and 70–75% RH (table 2).

Adult emergence

For *S. exigua*, the adult emergence rate varied with temperature and RH (model, $P < 0.0001$). Temperature ($P < 0.0001$) and RH ($P < 0.0001$) significantly impacted the adult emergence rate. However, the combined effects of temperature and RH were not significant ($P = 0.1461$). Adult emergence rate increased with increasing temperature and RH. The highest adult emergence rate was 61.52% (± 5.8 SE) at 30°C and 70–75% RH (fig. 2A).

For *S. litura*, the adult emergence rate varied with temperature and RH (model, $P < 0.0001$). Temperature ($P < 0.0001$) and RH ($P < 0.0001$) significantly impacted the adult emergence. Similarly, the combined effects of temperature and RH were also significant ($P = 0.0349$). Adult emergence rate increased with increasing temperature and RH. The highest adult emergence rate was 71.91% (± 5.4 SE) at 30°C and 70–75% RH (fig. 2B).

Adult longevity

For *S. exigua*, the adult longevity varied with temperature and RH (model, $P < 0.0001$). Temperature ($P < 0.0001$) and RH ($P < 0.0001$) significantly impacted the adult longevity. However, the combined effects of temperature and RH were not significant ($P = 1.0000$). The highest adult longevity was 12.86 days (± 0.2 SE) at 20°C and 70–75% RH (table 1).

For *S. litura*, the adult longevity varied with temperature and RH (model, $P < 0.0001$). Temperature ($P < 0.0001$) and RH ($P < 0.0001$) significantly impacted the adult longevity. However, the combined effects of temperature and RH were not significant ($P = 1.0000$). The highest adult longevity was 11.10 days (± 0.2 SE) at 20°C and 70–75% RH (table 2).

Discussion

The outcomes of this study suggest that both *Spodoptera* species could complete their life cycle on all tested temperatures and RH conditions. However, the influences of environmental conditions such as temperature and RH significantly varied on the life variables and adult performance of *Spodoptera* species. The present study shows that temperature emphatically affects all the life variables except for larval mortality, while RH affects all the life variables, such as oviposition, egg and larval survival, developmental period, adult emergence, and adult longevity, of both *Spodoptera* species. In addition to larval mortality and adult longevity for both *Spodoptera* species, combined effects of temperature and RH were recorded on the egg morality for *S. exigua* and adult emergence for *S. litura*.

Among the tested temperature and RH conditions, 30°C and 70–75% RH proved to be the furthermost optimal environmental conditions for fecundity and normal development of both *Spodoptera* species. We found that fecundity was emphatically decreased at minimal temperature. Previous studies reported that *Spodoptera* species laid a higher number of eggs at 25–30° C (Gupta *et al.*, 2007; Mehrkhou *et al.*, 2012; Jaba *et al.*, 2020),

Table 1. Temperature (20, 25, and 30°C) and relative humidity (30–35, 50–55, 70–75, and 90–95%) mediated egg and larva mortality (%), developmental period (days), and adult longevity (days) of *S. exigua* fed on an artificial diet

Life variables	Post-hoc analysis	Relative humidity (%)	Temperature (°C) 20	25	30	Post-hoc analysis for RH
Egg mortality		30–35	61.90 ± 5.8	47.14 ± 6.0	39.05 ± 5.9	a
		50–55	45.24 ± 6.0	41.43 ± 6.0	34.76 ± 5.8	b
		70–75	35.24 ± 5.8	29.52 ± 5.5	26.67 ± 5.4	c
		90–95	37.14 ± 5.9	25.24 ± 5.3	31.90 ± 5.6	c
	For temperature	–	A	B	B	
Larva mortality		30–35	22.67 ± 8.6	25.00 ± 7.4	23.70 ± 6.4	c
		50–55	39.17 ± 7.9	30.30 ± 7.0	24.49 ± 6.2	b
		70–75	23.61 ± 6.2	17.31 ± 5.3	20.13 ± 3.6	c
		90–95	57.97 ± 7.4	52.47 ± 6.9	60.13 ± 7.0	a
	For temperature	–	A	A	A	
Developmental period		30–35	51.01 ± 1.3	30.76 ± 0.3	20.19 ± 0.2	a
		50–55	49.77 ± 2.3	28.96 ± 0.3	18.88 ± 0.2	b
		70–75	47.88 ± 1.7	27.01 ± 0.2	16.49 ± 0.2	c
		90–95	47.38 ± 3.0	28.83 ± 0.2	18.80 ± 0.3	b
	For temperature	–	A	B	C	
Adult longevity		30–35	11.17 ± 0.4	9.39 ± 0.2	7.47 ± 0.2	c
		50–55	11.50 ± 0.3	9.85 ± 0.2	7.85 ± 0.2	b
		70–75	12.86 ± 0.2	10.05 ± 0.2	8.94 ± 0.3	a
		90–95	12.23 ± 0.5	8.77 ± 0.3	8.19 ± 0.3	b
	For temperature	–	A	B	C	

ANOVA for egg mortality: model: $F_{11, 2508}$ = 9.58; $P < 0.0001$, temperature: $F_{2, 2508}$ = 14.08; $P < 0.0001$, RH: $F_{3, 2508}$ = 21.74, $P < 0.0001$, and interaction: $F_{6, 2508}$ = 2.97, $P = 0.0400$. Larva mortality: model: $F_{11, 1617}$ = 17.11, $P < 0.0001$, temperature: $F_{2, 1617}$ = 2.19, $P = 0.1122$, RH: $F_{3, 1617}$ = 59.03, $P < 0.0001$, and interaction: $F_{6, 1617}$ = 1.12, $P = 0.3453$. Developmental period: model: $F_{11, 1068}$ = 4896.15, $P < 0.0001$, temperature: $F_{2, 1068}$ = 26,788.0, $P < 0.0001$, RH: $F_{3, 1068}$ = 10.92, $P < 0.0001$, and interaction: $F_{6, 1068}$ = 41.48, $P < 0.0001$. Adult longevity: model: $F_{11, 1063}$ = 135.70, $P < 0.0001$, temperature: $F_{2, 1063}$ = 657.45, $P < 0.0001$, RH: $F_{3, 1063}$ = 61.15, $P < 0.0001$, and interaction: $F_{6, 1063}$ = 0.00, $P = 0.0000$. Means (±SE) followed by the same capital letters in a row and same small letters in a column are not significantly different among temperature regimes and relative humidity levels, respectively (ANOVA, Tukey's [HSD] test, $P < 0.05$).

similar to our results. In the present study, *Spodoptera* species successfully laid eggs at a lower temperature (20°C), though it was the lowest number of eggs among the temperatures. In line with our findings, Choi and Park (2000) reported a lower number of eggs laid by *S. exigua* at a lower temperature (16°C). Nevertheless, Lee *et al*. (1991) reported a maximum number of eggs laid by *S. exigua* at a lower temperature (20°C). This fecundity discrepancy may be associated with relative humidity along with temperature. Several studies reported that different temperatures and RH have significant effects on the oviposition of *Spodoptera* species (Shuqing, 2002; Jaba *et al*., 2020).

Being a poikilothermic organism, insects are physiologically sensitive to external environmental factors, and temperature is the most significant factor influencing the overall developmental processes of insects (Taylor, 1981; Bale *et al*., 2002). Previous studies reported that RH affects the success of the egg hatchability of insect species (Holmes *et al*., 2012; Norhisham *et al*., 2013). Norhisham *et al*. (2013) reported that egg mortality was highest at lower RH levels in *Dinoderus minutus* Fabricius (Coleoptera: Bostrichidae). In line with earlier studies, we report here that there is higher egg mortality at lower (30–35%) rather than higher (90–95%) RH levels. Wigglesworth (1984) reported that water loss through the egg and pupal membranes due to low RH can be

responsible for inhibiting the survival and normal development of holometabolous insects, resulting in desiccation. We believe that the detrimental effects on egg eclosion success caused by lower RH could be associated with desiccation. This phenomenon is supported by Clark and Faeth (1997, 1998), where the authors noticed that eggs on the surface of egg clusters were desiccated, while eggs within the egg cluster were not. Previous studies indicated lower larval survival of *Spodoptera* species in higher temperature and RH (Jaba *et al*., 2020; Maharjan *et al*., 2023). In line with previous studies on *Spodoptera* species, we also found higher larval mortality in high humidity (90–95%) at all temperature regimes, and humidity levels (>90%) negatively affected larval survival. During microscopic observation, we noticed dead larvae with a higher amount of water within the larval body and fungal spores on the outer surface of the body. Thus, we believe that larval death could be caused by RH-assisted mould formation.

Earlier studies revealed that temperature and RH (Ranga Rao *et al*., 1989; Jaba *et al*., 2020; Rao and Prasad, 2020; Maharjan *et al*., 2022, 2023; Malekera *et al*., 2022) are potential factors influencing the life processes of *Spodoptera* species. A top of *Spodoptera* species, the influence of temperature and RH, and their interaction on the life variables of other insect species such as Spotted stem borer (*Chilo partellus*) (Lepidoptera:

Table 2. Temperature (20, 25, and 30°C) and relative humidity (30–35, 50–55, 70–75, and 90–95%) mediated egg and larva mortality (%), developmental period (days), and adult longevity (days) of *S. litura* fed on an artificial diet

Life variables	Post-hoc analysis	Relative humidity (%)	Temperature (°C)			Post-hoc analysis for RH
			20	25	30	
Egg mortality		30–35	58.10 ± 8.7	40.00 ± 5.9	34.76 ± 5.8	a
		50–55	38.57 ± 5.9	30.00 ± 5.5	28.57 ± 5.5	b
		70–75	30.95 ± 5.6	23.33 ± 5.1	25.24 ± 5.3	c
		90–95	35.71 ± 5.8	24.29 ± 5.2	28.10 ± 5.4	bc
	For temperature	–	A	B	B	
Larva mortality		30–35	21.11 ± 7.6	29.46 ± 7.1	25.00 ± 6.4	b
		50–55	33.33 ± 7.1	24.18 ± 6.1	22.64 ± 5.8	b
		70–75	20.92 ± 5.8	19.88 ± 5.4	21.21 ± 5.6	b
		90–95	46.94 ± 7.3	42.42 ± 6.8	53.46 ± 10.7	a
	For temperature	–	A	A	A	
Developmental period		30–35	48.46 ± 2.7	33.96 ± 0.4	28.64 ± 0.3	a
		50–55	46.32 ± 2.6	34.03 ± 0.3	26.86 ± 0.3	b
		70–75	44.74 ± 2.6	33.12 ± 0.2	25.61 ± 0.4	b
		90–95	46.03 ± 2.1	33.99 ± 0.2	27.81 ± 0.5	a
	For temperature	–	A	B	C	
Adult longevity		30–35	9.73 ± 0.2	7.90 ± 0.2	5.90 ± 0.2	c
		50–55	10.23 ± 0.3	7.76 ± 0.2	6.72 ± 0.2	b
		70–75	11.07 ± 0.3	8.72 ± 0.2	7.00 ± 0.1	a
		90–95	10.14 ± 0.3	8.18 ± 0.2	5.59 ± 0.2	b
	For temperature	–	A	B	C	

ANOVA for egg mortality: model: $F_{11, 2508} = 8.97$, $P < 0.0001$, temperature: $F_{2, 2508} = 17.44$, $P < 0.0001$, RH: $F_{3, 2508} = 17.95$, $P < 0.0001$, and interaction: $F_{6, 2508} = 1.66$, $P = 0.1262$. Larva mortality: model: $F_{11, 1737} = 12.54$, $P < 0.0001$, temperature: $F_{2, 1737} = 0.69$, $P = 0.5036$, RH: $F_{3, 1737} = 38.80$, $P < 0.0001$, and interaction: $F_{6, 1737} = 3.37$, $P = 0.0026$. Developmental period: model: $F_{11, 1222} = 1264.16$, $P < 0.0001$, temperature: $F_{2, 1222} = 6842.65$, $P < 0.0001$, RH: $F_{3, 1222} = 32.33$, $P < 0.0001$, and interaction: $F_{6, 1222} = 20.58$, $P < 0.0001$. Adult longevity: model: $F_{11, 1222} = 290.08$, $P < 0.0001$, temperature: $F_{2, 1222} = 1460.40$, $P < 0.0001$, RH: $F_{3, 1222} = 90.54$, $P < 0.0001$, and interaction: $F_{6, 1222} = 0.00$, $P = 1.0000$. Means (±SE) followed by the same capital letters in a row and same small letters in a column are not significantly different among temperature regimes and relative humidity levels, respectively (ANOVA, Tukey's [HSD] test, $P < 0.05$).

Crambidae) and rice weevil (*Sitophilus oryzae* L.) (Coleoptera: Curculionidae) was also reported by previous studies (Tamiru et al., 2012; Hasan et al., 2017). In line with the findings of these earlier studies, the findings of this study indicated that the developmental period of *Spodoptera* species was shorter with the increase in temperature. We also suggest here that the increment in RH from 30–35 to 70–75% reduced the developmental period and enhanced the adult emergence. However, extreme RH levels (lower (30–35%) and higher (>90%)) adversely impacted the emergence rate of adults, which is in agreement with Wigglesworth (1984), who reported that low RH results in water loss through egg cells and pupal membranes, which can lead to desiccation and be a detrimental means for the success of insect survival, which could also partly be linked to higher mortality of larvae driven by fungal infections. Further, the distinct effects of temperature and RH rather than the interactive effect might be responsible for the deleterious impact on the adult emergence. Earlier research indicated that temperature plays a more significant part than RH in the life processes of *Spodoptera* species (Ranga Rao et al., 1989; Bale et al., 2002). As with other life variables, temperature and RH also influenced the longevity of adult *Spodoptera* species (Ranga Rao et al., 1989; Rao and Prasad, 2020; Maharjan et al., 2022, 2023), which is in line with the findings of previous studies; we observed inverse

effects of temperature on adult longevity, and we found higher adult longevity of *Spodoptera* species in 70–75% RH at 20°C. Significant factors confirming insects' longevity are still unknown. Among the significant factors, temperature is considered as one of the most influential factors regulating the lifespan of insect species. In addition to temperature, genetic background, physiology and metabolic processes, and nutrients and chemical compounds available on host plants may also influence the adult longevity of insect species (Kenyon, 2010; Maharjan et al., 2022, 2023).

Here, we reported that both the temperature and the RH are significant factors that have central roles in the developmental processes and adult performance of *Spodoptera* species, however, the way that temperature and relative humidity interact depends on certain life variables of *Spodoptera* species. This study showed that a temperature of 30°C and RH of 70–75% were optimal conditions for overall development of *Spodoptera* species. Temperature had the greatest effect on the life variables of *Spodoptera* species, though the effect of RH was minimal with occasional statistical significance for some variables. This study suggests that immature stages (especially egg and larva) are more sensitive to RH. Information on egg and larval mortality indicates that the effect of RH is important when an insect is in an immature stage and in a stressed state due to adverse temperature. Further, the outcomes of this study demonstration that
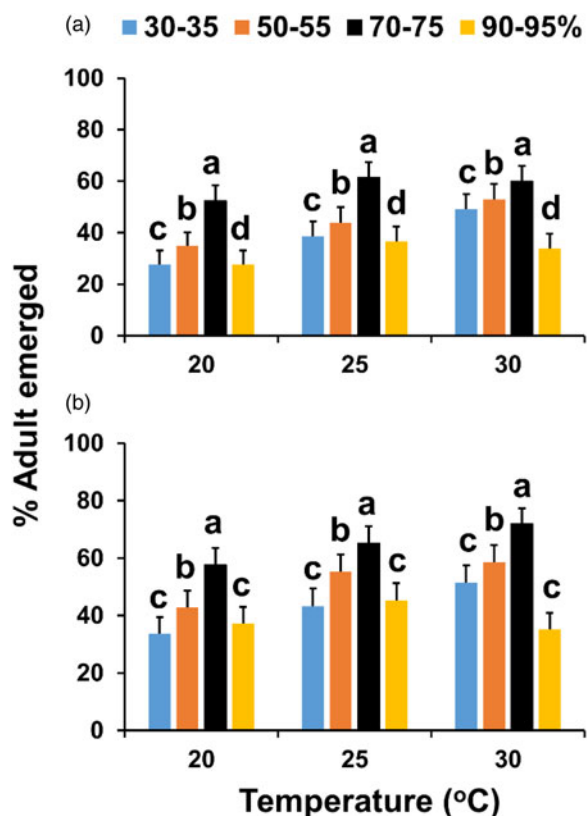
Figure 2. Temperature (20, 25, and 30°C) and relative humidity (30–35, 50–55, 70–75, and 90–95%) mediated adult emergence rate of *S. exigua* (A) and *S. litura* (B) fed on an artificial diet. Bars represent standard error. ANOVA for *S. exigua*: model: $F_{11, 2508} = 12.54$, $P < 0.0001$, temperature: $F_{2, 2508} = 16.95$, $P < 0.0001$, RH: $F_{3, 2508} = 31.52$, $P < 0.0001$, and interaction: $F_{6, 2508} = 1.59$, $P = 0.1461$. For *S. litura*: model: $F_{11, 2508} = 13.15$, $P < 0.0001$, temperature: $F_{2, 2508} = 13.17$, $P < 0.0001$, RH: $F_{3, 2508} = 34.92$, $P < 0.0001$, and interaction: $F_{6, 2508} = 2.27$, $P = 0.0349$. Means followed by the same letters are not significantly different among relative humidity levels (ANOVA, Tukey's [HSD] test, $P < 0.05$).

Spodoptera species are supposed to cause significant damage to the field crops and vegetables grown under environmental conditions (temperature around 30°C and 70–75% RH). Lastly, information generated from this study can be integrated with other management strategies for the management of *Spodoptera* species.

References

Ahmad M and Arif MI (2010) Resistance of beet armyworm *Spodoptera exigua* (Lepidoptera: Noctuidae) to endosulfan organophosphorus and pyrethroid insecticides in Pakistan. *Crop Protection* **29**, 1428–1433.

Ali A and Gaylor MJ (1992) Effects of temperature and larval diets on development of the beet armyworm. *Environmental Entomology* **21**, 780–786.

Bae SD (1999) Leaf characteristics of leguminous plants and the biology of tobacco cutworm, *Spodoptera litura* Fabricius: I. The larval development and leaf feeding amount. *Korean Journal of Applied Entomology* **38**, 217–224.

Bae SD, Park KB and Oh YJ (1997) The effects of temperature and food source on the egg and larval development of tobacco cutworm, *Spodoptera litura* Fabricius. *Korean Journal of Applied Entomology* **36**, 48–54.

Bale JS, Masters GJ, Hodkinson ID, Awmack C, Bezemer TM, Brown VK, Butterfield J, Buse A, Coulson JC, Farrar J, Good JEG, Harrington R, Hartley S, Jones TH, Lindroth RL, Press MC, Symrnioudis I, Watt AD and Whittaker JB (2002) Herbivory in global climate change research: direct effects of rising temperature on insect herbivores. *Global Change Biology* **8**, 1–16.

Bandoly M and Steppuhn A (2016) Bioassays to investigate the effects of insect oviposition on a plant's resistance to herbivores. *Bio-Protocol* **6**, e1823.

Brewer MJ and Trumble JT (1991) Inheritance and fitness consequences of resistance to fenvalerate in *Spodoptera exigua* (Lepidoptera: Noctuidae). *Journal of Economic Entomology* **84**, 1638–1644.

Choi JS and Park YD (2000) Effects of some temperatures on larval development, adult longevity, and oviposition of the beet armyworm, *Spodoptera exigua* Hübner. *Korean Journal of Life Science* **10**, 1–6.

Clark BR and Faeth SH (1997) The consequences of larval aggregation in the butterfly *Chlosyne lacinia*. *Ecological Entomology* **22**, 408–415.

Clark BR and Faeth SH (1998) The evolution of egg clustering in butterflies: a test of the egg desiccation hypothesis. *Evolutionary Ecology* **12**, 543–552.

Dai HQ, Zhang GL and Zhang WJ (2017) Temperature dependent development parameters and population life table of beet armyworm, *Spodoptera exigua* (Hübner) (Lepidoptera: Noctuidae). *Arthropods* **6**, 117–125.

Dhir BC, Mohapatra HK and Senapati B (1992) Assessment of crop loss in groundnut due to tobacco caterpillar, *Spodoptera litura* (F.). *Indian Journal of Plant Protection* **20**, 215–217. Available at https://api.semanticscholar.org/CorpusID:82790324

EPPO (2013) 2013 PQR Database: European and Mediterranean Plant Protection Organization, Paris, France. Retrieved from http://www.eppo.int/DATABASES/pqr/pqr.htm

EPPO (2015) *Spodoptera littoralis*, *Spodoptera litura*, *Spodoptera frugiperda*, *Spodoptera eridania*. *EPPO Bulletin* **45**, 410–444.

Fand BB, Sul NT, Bal SK and Minhas PS (2015) Temperature impacts the development and survival of common cutworm (*Spodoptera litura*): simulation and visualization of potential population growth in India under warmer temperatures through life cycle modelling and spatial mapping. *PLoS ONE* **10**, e0124682.

Goh HG, Lee SG, Lee BP, Choi KM and Kim JH (1990) Simple mass-rearing of beet armyworm, *Spodoptera exigua* (Hübner) (Lepidoptera: Noctuidae), on artificial diet. *Korean Journal of Applied Entomology* **29**, 180–183.

Greenberg SM, Sappington TW, Legaspi BCJ, Liu TX and Sétamou M (2001) Feeding and life history of *Spodoptera exigua* (Lepidoptera: Noctuidae) on different host plants. *Annals of the Entomological Society of America* **94**, 566–575.

Gupta GP, Rani S, Birah A and Raghuraman M (2007) Improved artificial diet for mass rearing of the tobacco caterpillar, *Spodoptera litura* (Lepidoptera: Noctuidae). *International Journal of Tropical Insect Science* **25**, 55–58.

Hasan M, Aslam A, Jafir M, Javed MW, Shehzad M, Chaudhary MZ and Aftab M (2017) Effect of temperature and relative humidity on development of *Sitophilus oryzae* L. (Coleoptera: Curculionidae). *Journal of Entomology and Zoology Studies* **5**, 85–90.

Holmes LA, Vanlaerhoven SL and Tomberlin JK (2012) Relative humidity effects on the life history of *Hermetia illucens* (Diptera: Stratiomyidae). *Environmental Entomology* **41**, 971–978.

Howe RW (1965) A summary of estimates of optimal and minimal conditions for population increase of some stored products insects. *Journal of Stored-Products Research* **1**, 177–184.

Hunter MD (2001) Effects of elevated atmospheric carbon dioxide on insect–plant interactions. *Agricultural and Forest Entomology* **3**, 153–159. Available at http://www.ecology.uga.edu./hunter.html

Jaba J, Mishra SP, Arora N and Munghate R (2020) Impact of variegated temperature, CO₂ and relative humidity on survival and development of beet armyworm *Spodoptera exigua* (Hübner) under controlled growth chamber. *American Journal of Climate Change* **9**, 357–370.

Jung JM, Byeon DH, Jung S and Lee WH (2019) Effect of climate change on the potential distribution of the common cutworm (*Spodoptera litura*) in South Korea. *Entomological Research* **49**, 519–528.

Kenyon CJ (2010) The genetics of ageing. *Nature* **464**, 504–512.

Kim CH and Shin HY (1987) Studies on bionomics and control of tobacco cutworm, *Spodoptera litura* Fabricius in southern part of Korea. *Journal of Institute of Agriculture and Resource Utility-Gyeongsang National University* **21**, 105–122.

Lai T and Su J (2011) Assessment of resistance risk in *Spodoptera exigua* (Hübner) (Lepidoptera: Noctuidae) to chlorantraniliprole. *Pest Management Science* **67**, 1468–1472.

Lee SD, Ahn SB, Cho WS and Choi KM (1991) Effects of temperature on the development of beet armyworm, *Spodoptera exigua* (Hübner) (Lepidoptera: Noctuidae). *Research Report of RDA, Crop Protection* **33**, 58–62.

Luo LZ and Cao YZ (2000) Studies on the *Spodoptera exigua* occurrence, damage characteristics and the trend analysis. *Plant Protection* **26**, 37–39.

Maharjan R, Ahn J and Yi H (2022) Interactive effects of temperature and plant host on the development parameters of *Spodoptera exigua* (Hübner) (Lepidoptera: Noctuidae). *Insects* **13**, 747.

Maharjan R, Hong S, Ahn J, Yoon Y, Jang Y, Kim J, Lee M, Park K and Yi H (2023) Temperature and host plant impacts on the development of *Spodoptera litura* (Fabricius) (Lepidoptera: Noctuidae): linear and nonlinear modeling. *Insects* **14**, 412.

Malekera MJ, Acharya R, Mostafiz MM, Hwang H-S, Bhusal N and Lee K-Y (2022) Temperature-dependent development models describing the effects of temperature on the development of the fall armyworm *Spodoptera frugiperda* (J. E. Smith) (Lepidoptera: Noctuidae). *Insects* **13**, 1084.

Mascarenhas VJ, Graves JB, Leonard BR and Burris E (1998) Susceptibility of field populations of beet armyworm (Lepidoptera: Noctuidae) to commercial and experimental insecticides. *Journal of Economic Entomology* **91**, 827–833.

Mehrkhou F, Talebi AA, Moharramipour S, Naveh VH and Farahani S (2012) Development and fecundity of *Spodoptera exigua* (Lepidoptera: Noctuidae) on different soybean cultivars. *Archives of Phytopathology and Plant Protection* **45**, 90–98.

Norhisham AR, Abood F, Rita M and Hakeem KR (2013) Effect of humidity on egg hatchability and reproductive biology of the bamboo borer (*Dinoderus minutus* Fabricius). *SpringerPlus* **2**, 9. PMID:23419805; PMCID: PMC3569590. https://doi.org/10.1186/2193-1801-2-9

Osorio A, Martínez AM, Schneider MI, Díaz O, Corrales JL, Avilés MC, Avilés GS and Pineda S (2008) Monitoring of beet army-worm resistance to spinosad and methoxyfenozide in Mexico. *Pest Management Science* **64**, 1001–1007. Available at http://hdl.handle.net/1854/LU-690619

Ranga Rao GV, Wightman JA and Ranga Rao DV (1989) Threshold temperatures and thermal requirements for the development of *Spodoptera litura* (Lepidoptera: Noctuidae). *Environmental Entomology* **18**, 548–551.

Rao MS and Prasad TV (2020) Temperature based phenology model for predicting establishment and survival of *Spodoptera litura* (Feb.) on groundnut during climate change scenario in India. *Journal of Agrometeorology* **22**, 24–32.

Saeed S, Sayyed AH and Ahmad I (2010) Effect of host plants on life-history traits of *Spodoptera exigua* (Lepidoptera: Noctuidae). *Journal of Pest Science* **83**, 165–172.

SAS Institute Inc. (2002) SAS Use's Guide. Statistics; SAS, Institute Inc., Cary, NC, USA.

Sharma AN, Gupta GK, Verma RK, Sharma OP, Bhagat S, Amaresan N, Saini MR, Chattopadhyay C, Sushil SN, Asre R, Kapoor KS, Satyagopal K and Jeyakumar P (2014) Integrated pest management package for soybean; Directorate of Plant Protection, Quarantine and Storage: Faridabad, India, p. 41.

Shuqing L (2002) Effect of temperature and humidity on the development of *Spodoptera exigua* (Hübner). *Journal of Huazhong (Central China) Agriculture University* **21**, 352–355.

Tamiru A, Getu E, Jembere B and Bruce T (2012) Effect of temperature and relative humidity on the development and fecundity of *Chilo partellus* (Swinhoe) (Lepidoptera: Crambidae). *Bulletin of Entomological Research* **102**, 9–15.

Taylor F (1981) Ecology and evolution of physiological time in insects. *American Naturalist* **117**, 1–23. Available at https://www.jstor.org/stable/2460694

Tshiala MF, Botai JO and Olwoch JM (2012) Leaf miner Agromyzid pest distribution over Limpopo Province under changing climate. *African Journal of Agricultural Research* **7**, 6515–6522.

Wigglesworth VB (1984) *Insect Physiology*. New York, NY: Cambridge University Press, p. 202.

Winston PW and Bates DH (1960) Saturated solutions for the control of humidity in biological research. *Ecology* **41**, 232–237.

Xue M, Pang YH, Wang HT, Li QL and Liu TX (2010) Effects of four host plants on biology and food utilization of the cutworm, *Spodoptera litura*. *Journal of Insect Science* **10**, 22.

Zheng XL, Cong XP, Wang XP and Lei CL (2011) A review of geographic distribution, overwintering and migration in *Spodoptera exigua* Hübner (Lepidoptera: Noctuidae). *Journal of the Entomological Research Society* **13**, 39–48. Available at https://www.entomol.org/journal/index.php/JERS/article/view/327