RESEARCH

Temperature- and CO2-Dependent Life Table Parameters of Spodoptera litura (Noctuidae: Lepidoptera) on Sunflower and Prediction of Pest Scenarios

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ABSTRACT. Predicted increase in temperature and atmospheric CO2 concentration will influence the growth of crop plants and phytophagous insects. The present study, conducted at the Central Research Institute for Dryland Agriculture, Hyderabad, India, aimed at 1) construction of life tables at six constant temperatures viz., 20, 25, 27, 30, 33, and 35 ± 0.5°C for Spodoptera litura (Fabricius) (Lepidoptera: Noctuidae) reared on sunflower (Helianthus annuus L.) grown under ambient and elevated CO2 (eCO2) (550 ppm) concentrations in open top chambers and 2) prediction of the pest status in near future (NF) and distant future (DF) climate change scenarios at major sunflower growing locations of India. Significantly, lower leaf nitrogen, higher carbon and biomass carbon-nitrogen ratio were observed in sunflower foliage grown under eCO2 over ambient. Feeding trials conducted on sunflower foliage obtained from two CO2 conditions showed that the developmental time of S. litura (Egg to adult) declined with increase in temperature and was more evident at eCO2. Finite (r) and intrinsic rates of increase (r0), net reproductive rate (R0), mean generation time (T), and doubling time (DT) of S. litura increased significantly with temperature up to 27–30°C and declined with further increase in temperature. Reduction of T was observed from maximum value of 58 d at 20°C to minimum of 24.9 d at 35°C. The DT of population was higher (5.88 d at 20°C and lower (3.05 d) at 30°C temperature of eCO2. The data on these life table parameters were plotted against temperature and two nonlinear models were developed separately for each of the CO2 conditions for predicting the pest scenarios. The NF and DF scenarios temperature data of four sunflower growing locations in India is based on PRECIS A1B emission scenario. It was predicted that increased r, r0, r, and R0 and reduced T would occur during NF and DF scenario over present period at all locations. The present results indicate that temperature and CO2 are vital in influencing the population growth of S. litura and pest incidence may possibly be higher in the future.

Key Words: phytophagous insect, developmental time, insect pest, climate change, PRECIS

Global mean surface temperature has increased since the 19th century, each of the past three decades has been warmer than all previous decades, with the decade of the 2000’s being the warmest so far. The increase in temperature between the average of the 1850–1990 period and the 2003–2012 period is 0.78 (0.72–0.85) °C and the amount CO2 in the atmosphere has grown by about 40% over preindustrial levels (IPCC Climate Change 2013). The impacts of predicted increases in global average surface temperatures and atmospheric CO2 concentrations on insect-plant interactions have been studied separately, only a few studies have considered them together (Murray et al. 2013). Temperature influences the developmental rate of insects significantly and has direct effects, whereas the effect of elevated CO2 (eCO2) is host-mediated and indirect (Hunter 2001). It is well known that developmental rates increase with temperature up to certain levels beyond which they usually decrease (Tshiala et al. 2012). The most predicted effects of climate change, i.e., increase in atmospheric temperature and CO2 concentration, will have a significant effect on agriculture in general and on herbivore insect populations in particular. Quantification of the relationship between insect population development and temperature is vital to predict population dynamics of the insect pests.

Sunflower (Helianthus annuus L.), is one of the most important edible vegetable oil crops in the world. Sunflower oil is a frying oil, light in taste, appearance, and contains typical vegetable tri-glycerides with vit E (http://en.wikipedia.org/wiki/sunflower). The Russian federation, Ukraine, Argentina, China, and France are the major sunflower growing countries (http://faostat.fao.org). India stands in the 14th position in the world production with an average annual production of 15.7 million tons (http://agricoop.nic.in) from 7.32 m ha area with an average yield of 7.06 kg per ha. It is an introduced crop in India and the pest complex is different from temperate regions. The tobacco caterpillar, Spodoptera litura Fab. (Lepidoptera: Noctuidae) is a major pest of sunflower (Basappa and Santh랄akhmi 2005) and causes significant yield losses. Larvae cause severe defoliation during flower initiation stage leading to reduced supply of assimilates to the capitulum thereby affecting floret and seed production (Sujatha and Lakshminarayana 2007). Temperature (Ranga Rao et al. 1989) and CO2 (Srinivasa Rao et al. 2012) are known to alter the growth and development of S. litura.

Life tables are important tools for understanding the population dynamics of insect pests and explain the impact of various factors on the growth, survival, and reproduction of insect populations. Variation of life table parameters of lepidopterans (intrinsic rate of increase r0, and finite rate of increase λ) with temperature (Hardev et al. 2013), larval host and diet (Sheng 1994) and eCO2 (Dyer et al. 2013) have been reported. Life table parameters of S. litura were altered substantially in peanut (Tuan et al. 2013) and in non-Bt cotton (Prasad and Sreedhar 2011) with temperature. Studies analyzing variation of life table parameters with both tempeara and CO2 have not been attempted. The objectives of our study were 1) to measure the effect of constant temperatures and eCO2 on life table parameters of S. litura on sunflower and 2) to predict the pest status during near future (NF) and distant future (DF) climate change scenarios.

Materials and Methods

Open Top Chambers. Two square open top chambers (OTC) of 4 × 4 × 4 m, were constructed at the Central Research Institute for Dryland Agriculture (CRIDA), Hyderabad (17.38° N; 78.47°E), one
for maintaining eCO2 at concentrations of 550 ± 25 ppm and another one for ambient CO2 (aCO2) concentrations (380 ± 25 ppm CO2). Chambers were replicated twice making a total of four OTCs for experimentation. Carbon dioxide gas was supplied to chambers and maintained at set levels using manifold gas regulators, pressure pipelines, solenoid valves, rotameters, a sampler, a pump, a CO2 analyzer, a PC-linked Program Logic Control (PLC) and Supervisory Control and Data Acquisition (SCADA). The fully automated control and monitoring system includes a CO2 analyzer PLC and SCADA programme with PC that enabled the maintenance of desired levels of CO2 within the OTCs. The system monitored continuously the concentration of CO2, temperature, and relative humidity (RH) within the OTCs. The air was sampled from the centre point of the chamber through a coiled copper tube, which can be adjusted to different heights as the crop grows.

Sunflower (Var. KBSH-1) seeds were sown in the month of June in the four OTCs at two different CO2 concentrations and crop plants were maintained during entire crop season till December.

**Biochemical Constituents of Sunflower Foliage.** Leaf tissue used in the feeding experiments was analyzed for carbon, nitrogen, and C: N ratio. To determine carbon and nitrogen concentrations, samples were dried at 80°C and subsequently ground to powder. Leaf weight and nitrogen were measured using a CHN analyzer (Model NA 1500N, Carlo Erba Strumentazione, Italy) using standard procedures (Jackson 1973).

**Insects.** Egg masses of *S. litura* were collected from the field and maintained at the entomology laboratory of CRIDA. The cultures were obtained from the parent GCM (Krishna Kumar et al. 2011). In this article, we refer to the corresponding versions of downscaled projections at a relatively smaller spatial resolution are available and the projections vary from the parent GCM (Krishna Kumar et al. 2011). In this article, we chose to use the projections obtained at a resolution of 50 × 50 km grid using the PRECIS where the daily data on maximum temperature, minimum temperature, and rainfall are available. The output for the A1B emission scenario showing ‘reasonable skill in simulating the monsoon climate over India’ (Krishna Kumar et al. 2011) was considered. A1B is ‘the most appropriate scenario as it represents high technological development, with the infusion of renewable energy technologies following a sustainable growth trajectory’ (MoEF 2012). The future temperature data thus obtained were classified into two categories viz., ‘NF consisting of 2.021–2.050 and DF consisting of 2.071–2.098. The daily data during the crop duration of 133 days commencing from 26 to 44 Standard Weeks was considered for predicting the life table parameters of *S. litura* in future as pest scenarios.

**Statistical Analysis.** The data on developmental rate of each stage of insect pest at six constant temperatures and two CO2 conditions were analysed by using one-way analysis of variance (ANOVA). Results presented are mean value of each determination (treatment) ± standard deviation (SD). The differences between mean values of treatments were determined by Tukey’s test and the significance was defined at P < 0.05. The mean values of life table parameters of *S. litura* across four locations for the three periods viz., present, near and future periods were compared using two-sample t-test assuming equal variances. The significance of mean values was defined at P < 0.01. All statistical analyses were done using SPSS version 16.0.
Table 1. Change in bio chemical constituents of sunflower foliage grown under eCO₂ and aCO₂

| Biochemical Constituents | eCO₂       | aCO₂       | F(P)      | LSD (P ≤ 0.05) |
|--------------------------|------------|------------|-----------|----------------|
| Nitrogen %               | 2.67 ± 0.10| 2.81 ± 0.12| 16.19     | 0.091          |
| Carbon %                 | 41.63 ± 0.95| 38.63 ± 0.83| 46.71     | 1.129          |
| C:N ratio                | 15.60 ± 0.42| 13.76 ± 0.59| 61.17     | 0.606          |

Means in the same column followed by different letter (a, b, c and d) are significantly different at P < 0.05 (ANOVA) by Tukey's test.

Effect of Temperature and CO₂ on Developmental Rate. The variation in developmental time for egg, larva, pupa, and adult stages of *Spodoptera litura* on sunflower at six constant temperatures at two CO₂ conditions is presented in Table 2. Reduction in average developmental time for the egg stage (F5,495 = 880.89; P < 0.01), larva (F5,295 = 1,288.50; P < 0.01), pupa (F5,270 = 93.72; P < 0.01), adult (F5,245 = 9.79; P < 0.01), and TLS (F5,295 = 26.04; P < 0.01) was observed with increase in temperature under both eCO₂ and aCO₂. The duration of all stages was shorter under eCO₂ than aCO₂ (Table 2). Decreased mean developmental time (days) of each stage, egg (from 7.61 to 3.32), larva (from 29.8 to 12.87), pupa (from 16.46 to 7.93), and adult (from 3.53 to 3.67), and TLS (from 39.2 to 27.8) from 20 to 35°C temperature on eCO₂ foliage. Survivorship of four stages of *S. litura* was akin to developmental rate and significant variation was observed with temperature increase at eCO₂. The highest (1.051) and lowest (1.013) survival rates from egg to adult were observed at 30 and 20°C temperature (Table 2).

Life Table Parameters. The data on life table parameters viz., *'rₘ'* , net reproductive rate (*'R₀'*), finite rate of increase (*'λ'*), and 'DT' at six constant temperatures with two CO₂ levels are shown in Table 3. The *'rₘ'* increased with increase in temperature from 20 to 30°C and declined with further increase in temperature. The *'R₀'* of *S. litura* was higher at 27°C temperature according to records obtained from observation of 1,056 offspring. Comparison of values of *'rₘ'* and *'R₀'* with temperature indicated a gradual increase to a maximum values. The reduction of *'T'* was observed from a maximum value of 58 days at 20°C to minimum of 24.9 days at 35°C and followed polynomial trend under eCO₂. The 'DT' which is the indicator of reproductive value of new eggs was found to be highest at 30°C and followed a decreasing trend with increase in...
The doubling time (DT) of population was highest (5.88 days) at 20°C and lowest (3.05 days) at 30°C temperature under eCO2 (Table 3). The results on two nonlinear models developed for eCO2 and aCO2 conditions separately are depicted in Figure 1a and b. The relationship between ‘r_m’ and temperature followed the polynomial/quadratic form and was found to be the best fit with $R^2$ in the range of $(R^2=0.899)$. A polynomial pattern was observed when the ‘R_o’ values were plotted against temperature ($R^2 = 0.896$) and the highest value was recorded at 21.48°C under eCO2. The highest values of ‘r_m’ were observed at 28.0°C for eCO2 (0.227) and 23.5°C for aCO2 (0.220). The reduction of ‘T’ and increase in ‘λ’ were observed at 33.28 and at 33.50°C, temperature respectively.

Fig. 1. (a) Relationship between temperature and life-table parameters (‘r_m’ and ‘R_o’) of Spodoptera litura on sunflower at eCO2 and aCO2. (b) Relationship between temperature and life-table parameters (‘T’ and ‘λ’) of Spodoptera litura on sunflower at eCO2 and aCO2.
The results showed that comparison within present period (0.96–0.99) at four locations. Increasing trend in NF (2.66–2.90) and DF (2.94–3.13) scenario in of females per female per day. At Bangalore location the negative value of 'r_m' increased to 0.14 from 0.13 in NF scenario. It was predicted that similar increases of 'r_m' would occur during DF scenario. The 'r' recorded an increasing trend in NF (2.66–2.90) and DF (2.94–3.13) scenario in comparison within present period (0.96 - 0.99) at four locations. Results showed that 'R_0' would be higher (602–911 offspring) during future climate change scenarios than during present period (486–525).

Table 4. Prediction of pest scenarios using life table parameters during NF and DF CCS at four sunflower growing locations

| Locations | Present | NF | DF |
|-----------|---------|----|----|
| Akola     | 0.02 ± 0.02 | 0.15 ± 0.00** | 0.15 ± 0.00** |
| Bangalore | (–0.05) ± 0.01 | 0.14 ± 0.00** | 0.15 ± 0.00** |
| Hayathnagar | 0.07 ± 0.01 | 0.15 ± 0.00** | 0.14 ± 0.00** |
| Raichur   | 0.03 ± 0.01 | 0.15 ± 0.00** | 0.14 ± 0.01** |

**The difference relative to the present period is significant at P < 0.01.

The 'T' of insect pest was found to decrease significantly during NF (1–2 d at three locations) and DF (5–6 d at all locations) climate scenarios.

The results of per cent change in predicted life table parameters during NF and DF scenarios over present climate period were calculated and are depicted in Figure 2. The per cent change in 'r_m' was higher at three locations under both NF and DF scenarios excepting Bangalore where negative 'r_m' values were predicted to occur indicating that the number of females per female would be reduced. The increase in 'R_0' was found to be higher in NF (50–70%) than DF (15–35%) at all four locations. The reduction of 'T' is expected to be higher in DF (11–18%) at four locations than NF scenario (1–7%). A minimal increase (2%) of 'T' would occur at Hyderabad during NF scenario. At all four locations 'l' was found to increase in both NF and DF by 69–230%.

**Discussion**

Plant growth and biochemical constitution varied with CO2 concentration causing a reduction in foliar nitrogen, which is the single most important limiting resource for phytophagous insects (Hunter 2001, Srinivasa Rao et al. 2012). Our results on biochemical analysis of sunflower foliage revealed a significant reduction (5%) of leaf nitrogen under eCO2 compared with aCO2 condition. In addition to this, most herbivorous insects appear to be negatively affected by eCO2 because of the reduction in foliar N and increase in C: N ratio. In our study, an 8% increase of ‘C’ and 13% increase in C: N ratio was observed under eCO2. Similar increase of C: N ratio was reported by De La Mata et al. (2013) for sunflower. The reduction in protein content and increase of C/N ratio in leaves under eCO2 (Bezemer and Jones 1998, Hunter 2001) imply changes in food quality which can influence insect growth and development.

Temperature is the most significant factor influencing growth and development of insects (Bale et al. 2002). The effects of temperature on insects are species specific. Generally lower temperatures result in a decrease in the rate of development and an increase in the duration of the time of each developmental stage. It is well known that the relationship between temperature and development in insects is linear over most of the normal operating, middle range of temperature, but
becomes sigmoid over the whole temperature range that permits development (Arbab et al. 2006). Earlier studies have revealed that the growth and development of S. litura are significantly influenced by temperature (Ranga Rao et al. 1989) and CO2 (Srinivasa Rao et al. 2012) on various hosts. The results of the present study showed that the developmental time of four stages of S. litura (Egg-adult) declined with increase in temperature on sunflower and was more evident at eCO2. The rate of development was lower at both lower (20°C) and higher temperatures (35°C) studied, signifying that the two extreme temperatures had adverse effects on growth of S. litura.

It is well known that insects do not live in stable environments with constant temperature; however the results of the present study under constant temperature are relevant in comprehending the dynamics of insect pests (Tshiala et al. 2012). Life table parameters showed that the \( r_m \) values of S. litura on eCO2 foliage are higher than those previously reported in the literature highlighting the significant influence of eCO2 in altering biochemical constituents, though Yin et al. (2010) observed a non-significant effect of eCO2 on \( r_m \) for cotton boll worms. In case of aphids, eCO2 influenced performance by producing an increase of \( r_m \), \( \lambda \), \( T \) and \( DT \) (Amirijami et al. 2012). Significant variation of \( r_m \) of S. litura with host plants and temperature was reported by Zhu et al. (2000) and Gedia et al. (2008).

Decrease of developmental time and increase in \( r_m \) of S. litura on eCO2 foliage was a non-linear polynomial relationship. Many empirical models incorporating \( r_m \) as a key parameter have been used for prediction of insect pest population dynamics. Temperature-driven phenology models developed using laboratory information and projections of future populations can be made (Vincent et al. 1997). The approach of using laboratory measurements of temperature was adopted by Tshiala et al. (2012) to model the empirical relationship between LT parameters and temperature and assess the impact of climate change on leaf miner population dynamics. The quantified relationship between life table parameters and temperature for S. litura for eCO2 foliage is higher than those previously reported in the literature highlighting the significant influence of eCO2 in altering biochemical constituents, though Yin et al. (2010) observed a non-significant effect of eCO2 on \( r_m \) for cotton boll worms. In case of aphids, eCO2 influenced performance by producing an increase of \( r_m \), \( \lambda \), \( T \) and \( DT \) (Amirijami et al. 2012). Significant variation of \( r_m \) of S. litura with host plants and temperature was reported by Zhu et al. (2000) and Gedia et al. (2008). The quantified relationship between life table parameters and temperature for S. litura were significantly influenced by temperature and CO2. Results from this study showed that both low and high temperatures limited the survival and development of this insect pest and the ideal condition for the growth was at 27°C temperature, while the developmental rate increases with temperature up to 30°C However the life table parameters are sensitive to temperature and CO2 which are the major factors of climate change. Our prediction of pest scenarios based on PRECIS A1B emission scenario data at four sunflower growing locations of India during NF and DF future climate change scenarios shows increase of \( r_m \) and \( \lambda \) with higher \( R_o \) and reduced \( T \) meaning that pest incidence would be higher in the future. These findings indicate that S. litura has potential to become even more damaging insect pest on sunflower as a result of climate change. Further investigations are required to quantify the role of biotic and other abiotic factors on possible predicted pest scenarios.

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References Cited

Abolmaty, S. M., A. A. Khalil, and A. M. H. Makkad. 2011. Using degree-day unit accumulation to predict potato tubeworm incidence under climate change conditions in Egypt. Nat. Sci., 9: 156–160.

Amirijami, A. R., H. S. Namaghi, and M. Shoor. 2012. The performance of Breviscoryne brassicae on ornamental cabbages grown in CO2 enriched atmosphere. J. Asia-Pacific Entomol. 15: 249–253.

Arbab, A., D. Kontodimas, and A. Sahragard. 2006. Estimating development of Aphis poni (DeGeer) (Homoptera: Aphiidae) using linear and nonlinear models. Entomol. 35: 1208–1215.

Bale, J. S., J. M. Gregory, D. H. Iann, A. T. Caroline, T. M. Bezemer, V. K. Brown, J. Butterfield, A. Buse, J. C. Coulson, and J. Farrar et al. 2002. Herbivory in global climate change research: direct effects of rising temperature on insect herbivores. Glob. Change Biol. 8: 1–16.

Basappa, H. and P. M. Santhalakshmi. 2005. Insect pests and diseases of sunflower and their management. Directorate of Oilseeds Research, Hyderabad, India, pp. 80.

Bezemer, T. M., and T. H. Jones. 1998. Long term effects of elevated CO2 and temperature on populations of the peach potato aphid Myzus persicae and its parasitoid Aphidius matricariae. Oecologia 116: 128–135.

Chi, H. 2005. TWO-SEX MS Chart; computer program for age-stage two-sex life table analysis. National Cheung Hsing University, Taichung, Taiwan. (http://140.120.197.173/ecology/prod/02.htm) (accessed 30 September 2013).

De la Mata, L., P. de la Haba, J. M. Alamillo, M. Pineda, and E. Aguera. 2013. Elevated CO2 concentrations alter nitrogen metabolism and accelerate senescence in sunflower (Helianthus annuus L.) plants. Plant Soil Environ. 59: 303–308.

Dyer, L. A., L. A. Richards, S. A. Short, and C. D. Dodson. 2013. Effects of CO2 and temperature on tritrophic interactions. PLoS ONE 8(4): e62528. doi: 10.1371/journal.pone.0062528.

Gedia, M. V., H. J. Vyas, M. E. Acharya, and P. V. Patel. 2008. Studies on life fecundity tables of Spodoptera litura (Fabricius) on groundnut. Ann. Plant Protect. Sci. 16: 74–77.

Hardev, S. S., N. Gareeg, E. W. Susan, H. G. Ronald, and A. G. Robert. 2013. Temperature-dependent reproductive and life table parameters of Elasmus lignosellus (Lepidoptera:Pyralidae) on sugarcane. Fla. Entomol. 96: 380–390.

Hirschi, M., S. Stoeckli, M. Dubrovsky, C. Spirig, P. Calanca, M. W. Rotach, A. M. Fischer, B. Duffy, and J. Samietz. 2012. Downscaling climate change scenarios for apple pest and disease modeling in Switzerland. Earth Syst. Dyn. 3: 33–47.

Hunter, M. D. 2001. Effects of elevated atmospheric carbon dioxide on insect plant interactions. Agric. Forest Entomol. 3: 153–159.

Jackson, M. L. 1973. Soil chemical analysis, 498. Prentice Hall of India Private Limited, New Delhi, India.

IPCC Climate Change. 2013. The physical science basis. Summary for policy makers. Contribution of working group I to the fifth assessment. Report of
the intergovernmental panel on climate change. IPCC Secretariat, WMO, Geneva, Switzerland. pp. 3.

Iranipour, S., A. K. Pakdel, and G. Radjabi. 2010. Life history parameters of the Sunn pest, Eurygaster integriceps, held at four constant temperatures. J. Insect Sci. 10: 106.

Krishna Kumar, K., S. K. Patwardhan, A. Kulkarni, K. Kamala, R. Koteswararao, and R. Jones. 2011. Stimulated projections for summer monsoon climate over India by a high-resolution regional climate model (PRECIS). Curr. Sci. 3: 312–326.

MoEF. 2012. Indian Second National Communication to the United Nations Framework Convention on Climate Change. Ministry of Environment and Forests, Government of India. pp. 319.

Murray, T. J., D. S. Ellsworth, D. T. Tissue, and M. Riegler. 2013. Interactive direct and plant-mediated effects of elevated atmospheric (CO2) and temperature on a eucalypt-feeding insect herbivore. Glob. Change Biol. 19: 1407–1416.

Prasad, J. V., and U. Sreedhar. 2011. Life parameters of tobacco caterpillar, Spodoptera litura as influenced by transgenic (bt) cotton hybrids. Indian J. Entomol. 73: 312–316.

Ranga Rao, G. V., J. A. Wightman, and D. V. Ranga Rao. 1989. Threshold temperatures and thermal requirements for the development of Spodoptera litura (Lepidoptera: Noctuidae). Environ. Entomol. 18: 548–551.

Sheng, O. Y. 1994. Life tables of tobacco cutworm Spodoptera litura (F). Chin. J. Entomol. 14: 183–205.

Srinivasa Rao, M., D. Manimanjari, M. Vanaja, C. A. Rama Rao, K. Srinivas, V. U. M. Rao, and B. Venkateswarlu. 2012. Impact of elevated CO2 on tobacco caterpillar, Spodoptera litura on peanut, Arachis hypogaea. J. Insect Sci. 12: 103.

Sujatha, M., and M. Lakshminarayana. 2007. Resistance of Spodoptera litura (Fabricius) In Helianthus species and backcross derived inbred lines from crosses involving diploid species. Euphytica 155: 205–213.

Tshiala, M. F., J. O. Botai, and J. M. Olwoch. 2012. Leafminer agromyzid pest distribution over Limpopo province under changing climate. Afr. J. Agric. Res. 7: 6515–6522.

Tuan, S. J., C. C. Lee, and H. Chi. 2013. Population and damage projection of Spodoptera litura (F) on peanuts (Arachis hypogaea L.) under different conditions using the age stage TWO-SEX life table. Pest Manag. Sci. 70: 805–813.

Vincent, P., H. M. Jones Carrie, and C. C. Tome Lois. 1997. Life tables for the Koa Seed worm (Lepidoptera: Tortricidae) based on Degree-Day Demography. Popul. Ecol. 26: 1291–1298.

Yin, J., Y. C. Sun, G. Wu, and F. Ge. 2010. Effects of elevated CO2 associated with maize on multiple generations of the cotton bollworm Helicoverpa armigera. Entomologia Experimentalis et Applicata 136: 12–20.

Zhu, S. Z., L. Lu, F. Chen, W. Yu, and S. J. Zhang. 2000. Effect of temperature and food on Spodoptera litura population. Chin. J. Appl. Ecol. 11: 111–114.

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