Effect of elevated temperature on life-history parameters of rice yellow stem borer (*Scirpophaga incertulas* Walker)

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A study was undertaken to understand the effect of increasing temperature on population dynamics of yellow stem borer (YSB), Scirpophaga incertulas. Experiments were carried out in a temperature control chamber with five different constant temperatures (28°C, 30°C, 32°C, 34°C and 36°C). The data on agespecific life table at varying temperature regimes revealed that the total lifespan of YSB extended to a maximum of 52 days at 28°C followed by 49 days at 30°C and 46 days at 32°C. In general, survival of the YSB decreased with increasing temperature. Preoviposition period for YSB also decreased with increasing temperature. However, the total number of eggs laid by YSB increased with increasing temperature. Also, 50% fecundity in YSB was recorded on 49.7 days after incubation at 28°C, whereas it was observed as early as 34.4 days at 36°C. All the growth parameters were observed to decrease at 36°C, which reveals that temperature increase above 34°C is detrimental to the development of YSB. The above results reveal that, if the global warming continues at the present phase, it will negatively influence YSB and the population growth will be severely affected in the near future.

Keywords: Global warming, life and fecundity tables, population dynamics, temperature regime, yellow stem borer.

RICE is the staple food for over half of the world's population. It provides 49% of dietary energy and 39% of dietary protein in the developing world¹. Rice is attacked by more or less 100 species of insect pests, among which 20 are of economic importance. A few species, however, do cause significant damage and are extremely important. The yellow stem borer (YSB), *Scirpophaga incertulas* Walker (Pyralidae: Lepidoptera) is one of the major pests in all rice-producing areas of Asia, and India in particular, and accounts for 6–10% loss in crop yield².

Climate change, especially temperature increase, will affect insect physiology, behaviour, development as well as species distribution and abundance, evidenced by changes in the number of generations per year, increasing survival rates in winter, and the earlier appearance of some insects³. The Earth's climate has warmed by approximately 0.74°C over the past 100 years with two main periods of warming - between 1910 and 1945, and from 1976 onwards⁴. The last assessment report from the Intergovernmental Panel on Climate Change (IPCC)⁵ predicts an increment in mean temperature from 1.1°C to 6.4°C toward the year 2100. It is certain that the projected warming will increase exposure opportunities of insects and other ectothermic species to high temperatures exceeding their upper physiological limits⁶. It is important to understand the response of insects to high temperature, as the temperature is important for their survival and population development. Hence, a study was undertaken to understand the effect of increasing temperature on life-history parameters of YSB.

Materials and methods

Study area

The study was conducted at the Agro Climate Research Centre (ACRC), Tamil Nadu Agricultural University, Coimbatore from 2010 to 2013. It is situated in the western zone of Tamil Nadu at 11°N lat. and 77°E long., at an elevation of 427 m amsl. It is generally a dry district with an average rainfall of 720.8 mm distributed in 47 rainy days. The mean annual maximum and minimum temperatures are 31.9°C and 21.4°C respectively (source: Principal Agrometeorological Observatory, ACRC). The methodology followed in the present study was adapted from Iranipour *et al.*⁷.

Temperature control chamber

Experiments were carried out in a temperature control chamber (TCC), where the temperature was controlled using a fogger and mist fan. The TCC has a total area of 25 sq. m ($5 \text{ m} \times 5 \text{ m}$) with a column height of 4 m and fabricated using galvanized steel pipes. The roofing and outer walls were constructed with polycarbonate material.

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Weather sensors for recording air temperature at any required interval were placed inside the chamber. Required levels of temperature can be maintained by giving commands through the control panel. Temperature was recorded at hourly interval by the sensor which was connected to a data logger. All these data will be automatically stored in the data logger storage module. The data logger was connected to a computer and the recorded data were downloaded to the computer using Emcon GH 485/2 software program at regular intervals. For the present study, five different constant temperatures (28°C, 30°C, 32°C, 34°C and 36°C) were considered.

Yellow stem borer

To obtain uniform cohort of population, *S. incertulas* was mass-cultured following the method described by Saxena *et al.*⁸. Primary culture was established by collecting the borer moths with a sweep net in the rice fields during the day. The collected moths placed in vials and brought to the laboratory, where they were confined in wooden cages. The adult moths were fed with 10% sucrose solution soaked in cotton wool. Rice seedlings (ADT 43) of 40–50-day-old plants were kept in the cage for oviposition. After oviposition, the egg mass deposited by the moths was collected by cutting-off the leaf section with eggs. The leaf sections were then placed on moist filter paper in petri dishes and stored at room temperature. The larvae hatched were used for further studies.

Observations

Data on vital schedules of survival, mortality and fecundity were collected for YSB at each temperature regime. The observations on fecundity and total number of females emerged were recorded from the experiment⁷. Using the above-mentioned observations, life and fecundity tables were constructed for different temperature regimes.

Experimental procedure for different observations: This study was carried out by collecting the female moths from mass culture of YSB and keeping them separately in each insect cage (height $-2^{3}/_{4}$ ft, width $-2^{1}/_{2}$ ft, length $-2^{1}/_{2}$ ft, netted on three sides) under different temperatures with one month duration of paddy crop for egg-laying. Date of egg-laying and hatching was recorded. Leaf with egg masses were kept in petri dishes in an incubator to maintain the temperature. Observations of the eggs were made till they hatched⁷.

On hatching, first instars of larvae were detected from the egg mass with the help of hand lens and collected using camel hair brush and kept separately by introducing them in a piece of rice stem, covered with moist cotton at one end to prevent drying. The rice stems with larvae inside were kept separately in test tubes of 5×1 cm size, plugged with cotton and all the tubes were placed under different temperature regimes. The stems with larvae were monitored daily for their development. Once the stem started to dry, the larvae were shifted to fresh piece of stem for their feeding and development. The stems were opened carefully without any damage to observe the pupated larvae. Once the larvae had pupated, they were kept out of the stem in test tubes after four days of pupation for easy observation of adult emergence. Mortality was recorded daily until their death⁷.

For fecundity of female adults, freshly emerged male and female moths were kept together in an insect cage with rice seedlings for mating. The pre-oviposition period was calculated by observing the first production of eggs by female moths after emerging from the pupal case⁷.

Age-specific life table construction

Temperature-dependent complete life tables for YSB are built by partitioning its life cycle into distinct development stages (e.g. eggs, larvae, pupae and adults), and by evaluating the development time and survival or mortality for each stage.

Survivorship: The proportion of live births that survive to the beginning of any age interval is defined as age-specific survivorship (l_x) . Proportion surviving to each life stage (l_x) can be found by dividing the number of individuals living at the beginning of each age (a_x) by the initial number of eggs (a_0) . The first survivorship value entered in any life table (l_0) is always 1.0; 100% of the individuals are observed at the first stage⁹. Subsequent values for l_x are calculated by dividing the number of individuals observed at a given stage by the original number of individuals (a_x/a_0) . Survivorship (l_x) is presented in the form of graph which can provide a visual representation of how it changes with age in a population and can be used to make quick assessments of differences between populations.

Fixation of survivorship curves: The probabilities of survival as a function of age of the insect pest follow a logistic pattern (type-III curve). Hence, fixation is done by Doesn't Use Derivative (DUD) method¹⁰ as follows

Probability of survival
$$(y) = \frac{1}{1 + \exp\left(\frac{x-a}{b}\right)}$$

where a is the day in which 50% mortality was recorded, b the intercept and x is the age (days).

Fecundity: Derived from the word fecund, fecundity (m_x) generally refers to the ability to reproduce. In

demography, fecundity is the potential reproductive capacity of an individual or population. In biology, the definition is more equivalent to fertility, or the actual reproductive rate of an organism or population, measured by the number of eggs¹¹. The eggs produced per surviving individual at each age (m_x) or individual fecundity, was measured as F_x (total number of eggs) divided by a_x (total number of eggs produced per original individual at each age $(l_x m_x)$ is an important value to consider in population studies.

Net reproductive rate: The average number of offspring that a female produces during her lifetime is called net reproductive rate (R_0) . If all females survive to the oldest possible age for that population, then R_0 would simply be the sum of the average number of offspring produced by females at each age. In real populations, however, some females die at every age. The net reproductive rate (R_0) for a set cohort is obtained by multiplying the proportion of females surviving to each age (l_x) by the average number of offspring produced at each age (m_x) , and then adding the products from all the age groups:

$$R_0 = \sum l_x m_x,$$

where $l_x m_x$ is equivalent to the number of offspring (normally females) per original females produced at the age interval x starting from *i* to ∞ .

A net reproductive rate of 1.0 indicates that a population is neither increasing nor decreasing, but exactly replacing its numbers. This rate indicates population stability. Any number below 1.0 indicates a decrease in population, while any number above 1.0 indicates an increase⁷.

Intrinsic rate of natural increase: The intrinsic rate of natural increase (r_m) is the actual rate of natural increase of a specific population under stable age distribution, multiplying in specific constant environmental condition with *ad libitum* access to space and food. This is also known as Malthusian parameter^{12,13}. Very simply, this can be understood as the number of births minus the number of deaths per generation time. To derive this value using a life table, the natural logarithm of the net reproductive rate is divided by the mean generation time

Intrinsic rate of natural increase (r_m)

$$=\frac{\text{Net reproductive rate }(R_0)}{\text{Generation time }(T)},$$

Values above zero indicate that the population is increasing; the higher the value, the faster the growth rate. If a population has an intrinsic rate of natural increase of zero, then it is said to have stable age distribution and is neither growing nor declining in numbers.

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Finite rate of increase: The finite rate of increase is the antilog of r_m (ref. 7)

$$\lambda = e^{r_m}$$
.

In some circumstances it might be useful to calculate the finite rate of increase, i.e. the number of times the population multiplies in a unit of time.

Mean generation time: The other value needed to calculate the rate at which the population can grow is the mean generation time (*T*). Generation time is the average interval between the birth of an individual and that of its offspring. To determine the mean generation time of a population, the age of the individuals (*x*) is multiplied by the l_x and m_x . This calculation is performed for each age group, and the values are added together and divided by R_0 to yield the result⁷.

$$T = \sum \left(\frac{l_x m_x}{R_0}\right),$$

Doubling time of population: This is the effective time necessary for doubling of population⁷ and is arrived at by the following formula

$$t=\frac{\ln 2}{r_m}.$$

Results

Development time

The data on age-specific life table at varying temperature regimes revealed that the total lifespan of *S. incertulas* extended to a maximum of 52 days at 28°C followed by 49 days at 30°C and 46 days at 32°C (Table 1). The longest development time of YSB was recorded at the lowest temperature and shortest at higher temperature.

Survivorship

The survival exhibited by YSB indicated that it belongs to type-III survivorship curve. In general, survival decreased with increasing temperature. The curve indicated that the mortality during early stage of the pest was higher at higher temperature regimes (34°C and 36°C) (Figure 1). The 50% mortality in YSB was recorded after 26.6 days of incubation at 28°C. However, it occurred as early as on 7.2 days at the temperature regime of 36°C followed by 11.5 days at 34°C, indicating that the higher temperature regimes are detrimental for YSB survival. Using the DUD method, survivorship curves of different temperature regimes were smoothened. Table 2 provides

	Temperature regime (°C)					
Parameter	28	30	32	34	36	
Development time	52	49	46	40	38	
Length of preoviposition (days)	3	3	3	2	1	
Age of first oviposition (days)	49	46	43	36	34	
Age of 50% oviposition (days)	49.7	46.5	43.6	36.5	34.4	
Age of last oviposition (days)	52	49	46	40	38	
Age of maximum oviposition (days)	50	47	44	37	35	
Length of oviposition (days)	4	4	4	5	5	
Net reproductive rate (R_0 ; females/female)	24.16	33.26	30.09	18.24	7.01	
Intrinsic rate of natural increase $(r_m; day^{-1})$	0.06338	0.07404	0.07692	0.07795	0.05514	
Finite rate of increase (λ ; day ⁻¹)	1.0654	1.07685	1.07996	1.08107	1.05669	
Mean generation time (T; days)	50.25	47.33	44.26	37.25	35.32	
Doubling time (<i>t</i> ; days)	10.94	9.36	9.01	8.89	12.57	

 Table 1.
 Life table parameters of yellow stem borer at different temperature regimes



Figure 1. Age-specific survivorship of yellow stem borer (YSB) at different temperature regimes.

Table 2. Response of survival of YSB at different temperature regimes

Temperature regime (°C)	<i>a</i> (50% mortality)	b (intercept)	r^2 value
28	26.6	1.401	0.843
30	27.8	1.395	0.807
32	25.5	1.354	0.844
34	11.5	1.314	0.927
36	7.2	1.286	0.912

the parameters (a and b) of the smoothened curves of different temperature regimes.

Fecundity

Pre-oviposition period for YSB was found to decrease with increasing temperature. It was observed as 3 days at 28°C. Female adults started laying eggs after three days of emergence from the pupa. The pre-oviposition period was only one day at 36°C (Table 1). This indicated that the adult started laying eggs early at higher temperature than at lower temperature. The oviposition period of YSB adult indicated that the period of egg-laying increased with increasing temperature. From 28°C to 32°C, oviposition period was four days, whereas it was five days at 34°C and 36°C (Table 1). This indicated that the oviposition started early and continued for more number of days at higher temperature regime than at lower temperature regime. Age at first and last egg-laying was observed to be the 49th and 52nd days respectively, at 28°C. At 36°C, they were recorded on the 34th and 38th days respectively.

The total number of eggs laid by YSB increased with increasing temperature. Gross reproductive rate recorded was more (172) at 36°C and less (139) at 30°C (Figure 2). It was also noted that the 50% fecundity in YSB was recorded on 49.7 days after incubation at 28°C, whereas it was observed as early as on 34.4 days when YSB was reared at 36°C (Figure 3).



Figure 2. Cumulative fecundity of YSB at different temperature regimes.



Figure 3. Percentage of cumulative fecundity of YSB at different temperature regimes.

Net reproductive rate

 R_0 of YSB was more at lower temperature regimes of 28°C and 30°C. R_0 was observed to decrease at higher temperature regimes. The highest R_0 of 33.26 females/female was recorded at 30°C and lowest of 7.01 females/female was recorded at 36°C (Table 1).

Population growth parameters

Intrinsic rate of natural increase: The intrinsic rate of natural increase (r_m) increased with rise in temperature. It was 0.07795/day at 34°C, whereas it was 0.06338/day at 28°C. However, the increase in r_m had reversed after 34°C and hence, at 36°C it had been reduced to 0.05514/day (Table 1).

Finite rate of increase: The finite rate of increase (λ) also followed the same trend as r_m . λ increased with surging temperatures. It was 1.08107/day at 34°C, whereas it was 1.0654/day at 28°C. However, the increase in λ had

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reversed after 34° C and hence at 36° C it had been reduced to 1.05669/day (Table 1).

Doubling time: The doubling time (days) decreased with increasing temperature. It was 8.89 days at 34° C, whereas it was 10.94 days at 28° C. However, the decrease in doubling time had reversed after 34° C and hence at 36° C it had increased to 12.57 days (Table 1).

Mean generation time: YSB took 50.25 days at 28° C to complete the generation, which was longest of all the temperature regimes (Table 1). But it took only 35.32 days at 36° C, which was shortest of all the temperature regimes.

Discussion

Generation time

The generation time for YSB was lengthy at lower temperature regimes and shorter at higher temperature regimes. Temperature is a crucial factor, which wields a heavy effect on the growth of insects. Researchers have reported that the development time is positively correlated with temperature¹⁴.

Survivorship

Survivorship (l_x) diminished with increasing temperature. The time taken for 50% mortality also decreased with increasing temperature. This indicated that most of the insects reared under higher temperature regimes died faster and earlier as they were not able to tolerate higher temperatures. It was also reported that only 12.5% of nymphs survived when the temperature increased from 10°C to 35°C in *Tetraneura nigriabdominalis*¹⁵.

Fecundity

The longer pre-oviposition period at lower temperature perhaps assigned to the lower metabolic activity at lower temperature regimes¹⁶. Insects need to accumulate more energy to maintain the vital functions. Hence, at lower temperature pre-oviposition period was found to be more. However, the pre-oviposition period decreased when the insects lived at higher temperature regimes^{17–19}. But, when the temperature increased beyond the upper threshold level of the insects, all the growth and development processes were delayed.

The total number of eggs registered normally increased with increasing temperature. Ju *et al.*¹⁹ showed that the pre-oviposition period had a profound effect on the total number of eggs laid by the insects. Normally pre-oviposition period was shortened with increasing temperature (till the upper threshold limit) which led to higher number of eggs at higher temperature regimes.

Net reproductive rate

 R_0 decreased at higher temperature regimes²⁰. The results revealed that the reproduction rates of the green peach aphid were in general higher at temperatures between 20°C and 27.5°C (79.29–85.33 aphids aphid⁻¹) and decreased with an increase in temperature to 5.00 aphids aphid⁻¹ at 30°C. The lowest R_0 at elevated temperature was due to the highest mortality of the insects at early life stages²¹.

Population growth parameters

Intrinsic rate of natural increase, finite rate of increase and doubling time are regarded as population growth parameters. Population demographic parameters are important in measurement of population growth capacity of an insect under specified condition. It was reported that, developmental time decreased as temperature increased. This is the main reason why r_m was observed to increase with temperature in the present study²². As pointed out by Lewontin²³, and Dent and Walton²⁴, r_m is affected more by age of first reproduction than by fecundity. Delayed development causes a delay in onset of reproduction and a parallel increase in generation time.

Earlier egg production would contribute more to r_m (ref. 12). Thus, the higher r_m value might be attributed to the earlier oviposition at higher temperature regimes for all the pests. Correlation and regression analysis between r_m and fecundity indicated that there is an insignificant positive relationship (r = 0.2288; $r^2 = 0.052$). However, the results also revealed that the increase in r_m was not continuous as it reduced at 36°C (refs 15, 25). The lowest r_m value 36°C could be explained due to the heavy mortality at the highest temperature regime.

Conclusion

The survivorship pattern observed at different temperatures indicated that the young and immature stages was more susceptible to elevated temperatures. The survivorship curve revealed a faster rate of mortality during the early life stages and a gradual decrease as it approached adulthood; it assumed a near type-III survivorship curve. The results of the experiments revealed that, population growth parameters increase with increasing temperature. From this, it can be understood that the population of YSB is not in any danger due to the rise in temperature as projected in the future. However, the population of YSB would be under stress, if the temperature increase is beyond the upper threshold limit. As all the growth parameters were observed to decrease at 36°C, it can be concluded that the temperature increase above 34°C is detrimental to the development and survival of YSB.

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Errata

Understanding transitions in a rural Indian building typology in the context of well-being

Kumari Moothedath Chandran, Nallaval Chinnaswamy Balaji and Monto Mani [*Curr. Sci.*, 2015, **109**(9), 1610–1621].

Page 1613, para 3, line 9: read 'Durayappah' lists...' instead of 'Durayappa' lists...'

Page 1614, para 5, lines 2 & 3: read 'Deci and Ryan's²⁶...' instead of 'Ryan and Deci' s²⁷...'

Page 1614, para 6, line 1: read 'Deci and Ryan's²⁶ theory...' instead of 'Ryan's and Deci's²⁷ theory...'

Page 1616 bottom last paragraph: A significant part is verbatim from Reference 35 quoting Reference 34. The paragraph could thus read corrected as: 'Well-being is important in the thinking of a benefactor and in moral argument because of its importance for the individual whose well-being it is'^{34,35}. Rodogno³⁵ quotes Scanlon³⁴ on whether wellbeing is important to the individual whose well-being it is, as: '(a) It sounds absurd to say that individuals have no reason to be concerned with their own well-being, (b) because this seems to imply that they have no reason to be concerned with those things that make their lives go better. (c) Clearly they do have reason to be concerned with these things. (d) But in regard to their own lives they have little need to use the concept of well-being itself, either in giving justifications or in drawing distinctions... The concept of one's overall well-being does not play as important a role as it is generally thought to do in the practical thinking of a rational individual.'

Page 1620, ref. 9: read 'Durayappah, A.,' instead of 'Durayappa, A.,'

We regret the errors.

-Authors