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Effect of temperature on life history parameters of brown planthopper(*Nilaparvata lugens* Stal)

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Climate change, especially temperature increase, would affect insect physiology, behavior, and development as well as species distribution and abundance, evidenced by changes in the number of generations a year, increasing survival rates in winter, and the earlier appearance of some insects. Hence, an investigation was undertaken to understand effect of elevated temperature on population dynamics of Brown Planthopper (BPH). Experiments were carried out in Temperature control chamber (TCC) with five different constant temperatures (28.0, 30.0, 32.0, 34.0 and 36.0°C). Age specific life table was constructed for *Nilaparvata lugens* at various temperature regimes and it revealed that BPH took as long as 44 days to complete the generation at 28.0°C and as short as 32 days at 36.0°C. The 50% mortality occurred on 20.1 days after incubation at 28.0°C, whereas it was observed as early as on 6.3 days at 36.0°C. Pre-oviposition period decreased considerably with increasing temperatures. Total number of eggs recorded was more (233) at 30.0°C and less (116) at 36.0°C. It was also noted that the 50% fecundity in BPH was recorded on 36th day after incubation at 28.0°C, whereas it was observed on 24.3 days itself when the BPH was reared at 36.0°C. The net reproductive rate of BPH was observed to be higher at lower temperature regimes. All the growth parameters were observed to decrease at 36°C, which reveals that the temperature increase above 34 °C is detrimental to the development of BPH.

Key words: Global warming, temperature, life table, population growth, population dynamics.

INTRODUCTION

Rice is the most important food crop with more than 90% of global production occurring in tropical and semi-tropical Asia. In several Asian countries, rice provides between 50 and 70% of the energy and protein dietary requirements. The rapid acceleration of rice production over the last three decades has been a primary contributor to improvements in world food security (FAO, 2012). However, there are still 800 million people suffering from food deficits, which are further increased by the insect pest problems. Losses due to insect damage are likely to increase as a result of changes in crop diversity and increased incidence of insect pests due to temperature increase up to certain limit.

Insects flourish in all climates. It is reported that among

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all the climatic factors, temperature has probably the greatest effect on insect development (Bale et al., 2002). Climate change, especially temperature increase, will affect insect physiology, behavior, and development as well as species distribution and abundance, evidenced by changes in the number of generations a year, increasing survival rates in winter, and the earlier appearance of some insects (Huang et al., 2010). The duration of the immature stages and the time required to complete the cycle from egg to adult of Diamondback moth (*Plutella xylostella*) were significantly affected by temperature (Marchioro and Foerster, 2011). With temperatures within their viable range, insects respond to higher temperature with increased rates of development, more number of generations with less time between generations. Very high temperatures reduce insect longevity (Das et al., 2011). The population dynamics of the insect pests is expected to change with elevated air temperature influenced by global warming (Kwon et al., 2012). Hence, an investigation was undertaken to understand effects of increasing temperature on population dynamics of Brown Planthopper (BPH), *Nilaparvatalugens* (Stal) which is one of the major pests and has in recent years caused extensive damage to the rice crop in Asia.

MATERIALS AND METHODS

Study area

The study was conducted at Agro Climate Research Centre, Tamil Nadu Agricultural University, Coimbatore from 2010 to 2013. It is situated in the western zone of Tamil Nadu state at 11° N latitude and 77° E longitude and at an elevation of 427 m above the mean sea level. 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 and 21.4°C, respectively.

Temperature control chamber

Experiments were carried out in temperature control chamber (TCC), where temperature was controlled using fogger and a mist fan. The TCC has a total area of 25 m^2 (5 m × 5 m) with a column height of 4m and fabricated using galvanized steel pipes. The roofing and outer walls are constructed with polycarbonate material. Weather sensors for recording air temperature at any required interval are 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 and the sensor was connected to a data logger. All these data will automatically be stored in the data logger storage module. The data logger is connected to the computer and the data recorded is downloaded to the computer by Emcon GH 485/2 software program at regular intervals. For this investigation, five different constant temperatures (28.0, 30.0, 32.0, 34.0 and 36.0°C) with three replications were considered.

Brown planthopper (BPH)

BPH was mass reared separately on the susceptible rice variety ADT 43 as outlined by Heinrichs et al. (1985). Initial population was collected from the rice fields at Paddy Breeding Station, TNAU, Coimbatore. Adults were confined on 30 day old potted plants of ADT 43 placed in wooden wire netted and glass topped oviposition cages. The insects were removed three days after oviposition and the potted plants with eggs were collected and placed in separate cages to allow the eggs for nymphal emergence. The emerged nymphs were transferred to 15 day old ADT 43 rice seedlings raised in germination trays and these in turn were placed in galvanized iron (GI) trays (62 × 47 × 15 cm) containing 5 cm depth of water. ADT 43 seedlings in trays were changed periodically and thus continuous pure cultures of planthoppers were maintained. The nymphs hatched were used for the studies.

Observations

Data on vital schedules of survival, mortality and fecundity were collected for BPH at each temperature regime. The observations on fecundity and total number of females emerged were recorded from the experiment. By using the above said observations life and fecundity tables were constructed for BPH at different temperature regimes. The methodology followed in the present investigation was adopted from Iranipour et al. (2010).

Experimental procedure for different observations

This study was carried out first by collecting the female nymphs from mass culture and these nymphs were kept separately in each insect cage (Height-0.84 m, Width - 0.77 m, Length - 0.77 m, Netted in three sides) under different temperature regimes with a month duration of paddy crop for egg laying. Date of egg laying and hatching was recorded. Egg masses with leaf sheath were kept in Petri dishes in incubator to maintain temperatures. To prevent drying, the one end of which was covered with moist cotton. Observations of these eggs were made till they hatched.

On hatching, nymphs of first stage were detected from the egg mass and collected with the help of camel hair brush and kept separately with rice stem, covered with moist cotton at one end to prevent drying. The rice stem with nymph 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 nymphs were monitored daily and provided with fresh plant materials for their development. Mortality was recorded daily until their death.

For fecundity of female adults, freshly emerged male and female adults were kept together in an insect cage with rice seedlings for mating. The pre oviposition period was calculated by observing the first laying of eggs by female adults after the completion of nymphal stages.

Age specific life table construction

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

Survivorship (l_x)

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; one hundred percent of the individuals are

observed at the first stage (Priyanga and Romina, 2012). 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 survivorship in a population changes with age and can be used to make quick assessments of differences between populations.

Fixation of survivorship curves

The probabilities of survival in function of age of insect pest follow logistic pattern (Type III curve). Hence fixation by Doesn't Use Derivative (DUD) method (Raltson and Jenrich, 1978), using the following equation.

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

Where, a isday in which 50% mortality recorded; b isintercept; x isage (days).

Fecundity (m_x)

Fecundity derived from the word fecund, 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 eggs (Fox, 1993). The eggs produced per surviving individual at each age (m_x) or individual fecundity, were measured as F_x (Total number of eggs) divided by a_x (Total number of female). The 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 as net reproductive rate (R_o). If all females survived to the oldest possible age for that population, the net reproductive rate 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 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:

$R_0 = \Sigma\, l_x m_x$

Where, Ro is Net reproductive rate, and $l_x m_x$ is equivalent to the number of offspring (normally females) per original females produced at the age interval '*x'* starting '*i*' to '∞'

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

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 where space and food are *ad libitum*. It is also known as Malthusian parameter (Birch, 1948; Carey, 1993). Very simply, this rate 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:

$$\text{Intrinsic rate of natural increase } (r_m) = \frac{\text{Net reproductive rate } (R_0)}{\text{Generation time (T)}}$$

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.

Finite rate of increase (λ)

The finite rate of increase is the antilog of the intrinsic rate (infinitesimal) increase.

$\lambda = e^{r_m}$

It is useful to calculate the finite rate of increase as in indicates the number of times the population multiplies in a unit of time.

Mean generation time (T)

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 the birth of its offspring. To determine the mean generation time of a population, the age of the individuals (*x*) is multiplied by the proportion of females surviving to that age (l_x) and the average number of offspring left by females at that age (m_x). This calculation is performed for each age group, and the values are added together and divided by the net reproductive rate (R_o) to yield the result.

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

Where, $R_o$isnet reproductive rate, and $l_x m_x$ is equivalent to the number of offspring (normally females) per original females produced at the age interval '*x'* starting '*i*' to '∞'.

Doubling time of population (t)

It is the effective time necessary for doubling of population and is arrived at by the following formula

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

r_m is intrinsic rate of natural increase.

RESULTS

Development time

Age specific life table was constructed for *N. lugens*at

Table 1. Life table parameters of BPH at different temperature regimes.

Parameter	28.0°C	30.0°C	32.0°C	34.0°C	36.0°C	SED	CD (0.05)
Actual generation time (days)	44.0	44.0	40.0	33.0	31.0	1.077	2.48
Life expectancy (e_x) (days)	19.14	20.60	18.48	12.30	10.51	0.477	1.099
Pre-oviposition period	5	4	4	3	2	0.107	0.248
Age of first oviposition (day)	32	31	29	23	21	0.768	1.772
Age of 50% oviposition (day)	36	35.4	32.5	26.3	24.3	0.871	2.008
Age of last oviposition (day)	43	42	39	33	31	1.047	2.414
Age of maximum oviposition (day)	35	35	31	24	22	0.843	1.944
Length oviposition (days)	12	12	11	11	11	0.306	0.706
Net Reproductive rate (R_o) (females/female)	36.02	39.95	32.03	16.33	8.84	0.877	2.021
Intrinsic rate of natural increase (r_m) (day^{-1})	0.1011	0.1062	0.1083	0.1091	0.0935	0.002	0.006
Finite rate of increase (λ) (day^{-1})	1.1064	1.1121	1.1144	1.1153	1.0980	0.029	0.067
Mean generation time (T) (days)	35.46	34.72	32.00	25.59	23.30	0.854	1.970
Doubling time (t) (days)	6.86	6.53	6.40	6.35	7.41	0.177	0.409

Results are the means of three replications; CD, Critical difference; SED, standard deviation.

various temperature regimes and it revealed that BPH took as long as 44 days to complete the generation at 28.0°C and as short as 31 days at 36.0°C. The time taken for the development was inversely proportional to increasing temperatures (Table 1).

Survivorship (l_x)

The graph constructed by using the age specific survival of BPH indicated that it belongs to type III survivorship curve (Figure 1). The data revealed that the number of survivors decreased with the progress of time. During the early stage of the insects the curve was observed to dip steeply at higher temperature regimes as the mortality during early stage of the insect was higher at higher temperature regimes. The 50% mortality occurred on 20.1 days after incubation at 28.0°C, whereas it was observed as early as on 6.3 days at 36.0°C (Figure 1). This revealed that, BPH died earlier and faster at higher temperature regimes. Using the Doesn't Use Derivative (DUD) method, survivorship curves of different temperature were smoothened. Parameters (a and b) of the smoothened curves of different temperature regimes are given in Table 2.

Fecundity

Pre-oviposition period decreased considerably with increasing temperatures. It was observed to be five days at 28.0°C, but only 2 days at 36.0°C. There was a decrease in the oviposition period when the temperature increased. The oviposition period was 12 days at 28.0 and 30.0°C and 11 days at the remaining temperature regimes (Table 1). It indicated that the adults at higher temperature started laying their eggs earlier and completed the egg laying earlier, than the insects reared at lower temperature regimes. Age of first and last oviposition was observed to be 32^{nd} and 43^{rd} day respectively, at 28.0°C. At 36.0°C, they were recorded on 21^{st} and 31^{st} day, respectively (Table 1). The gross reproductive rate decreased at the higher temperature regimes. Total number of eggs recorded was more (233) at 30.0°C and less (116) at 36.0°C (Figure 2). It was also noted that the 50% fecundity in BPH was recorded on 36^{th} day after incubation at 28.0°C, whereas it was observed on 24.3 days itself when the BPH was reared at 36.0°C (Figure 3).

Net reproductive rate (R_o)

The net reproductive rate of BPH was observed to be higher at lower temperature regimes (28.0 and 30.0°C) of the experiment and lesser at higher temperature regimes. The highest R_o of 39.95 females/female was recorded at 30.0°C followed by 36.02 females/female at 28.0°C and the lowest R_o of 8.84 female/female was recorded at 36.0°C followed by 16.33 females/female at 34.0°C (Table 1).

Population growth parameters

Intrinsic rate of natural increase (r_m)

The intrinsic rate of natural increase (r_m) increased with increasing temperatures. It was 0.1091/day at 34.0°C, whereas it was 0.1011/day at 28.0°C. However, the increase in r_m has a turnaround after 34.0°C and hence at 36.0°C, r_m has been reduced to 0.09353/day (Table 1).

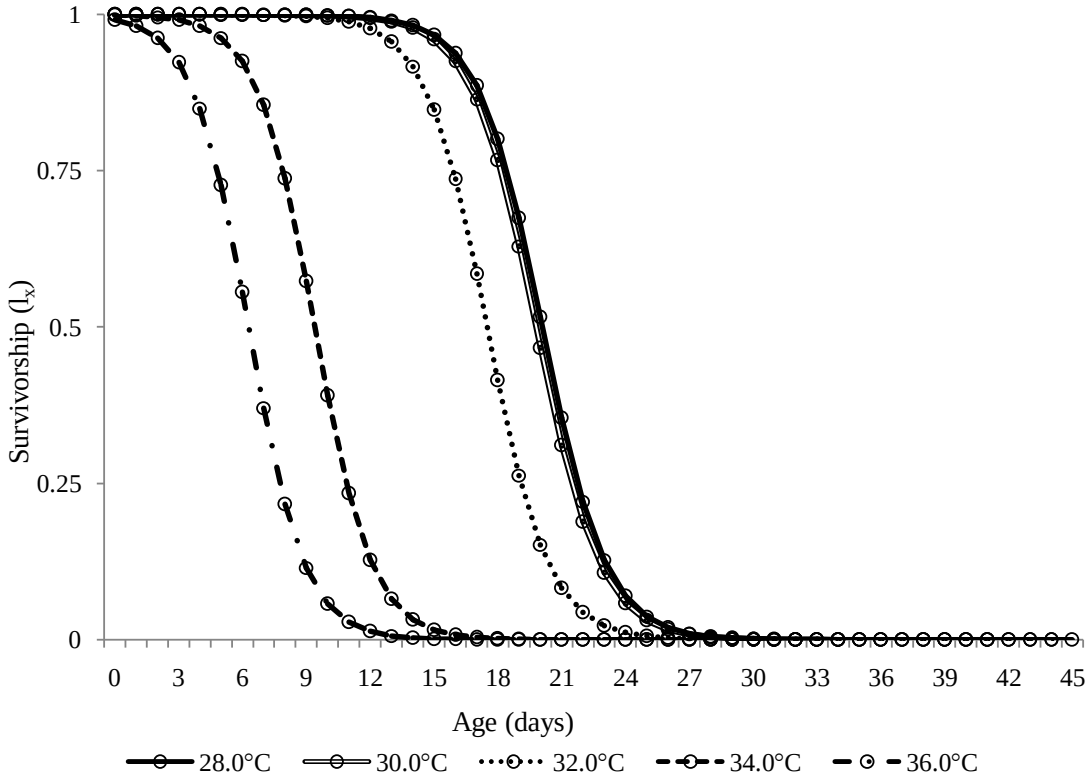

Figure 1. Age specific survivorship of BPH at different temperature regimes.

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

Temperature regimes	'a' (50% mortality)	'b' (Intercept)	r^2 Value
28.0°C	20.1	1.510	0.831
30.0°C	19.8	1.510	0.829
32.0°C	17.5	1.456	0.866
34.0°C	9.4	1.351	0.907
36.0°C	6.3	1.325	0.893
SED	0.4622		
CD (0.05)	1.0659		

Results are the mean of three replications. r^2, Regression coefficient.

Finite rate of increase (λ)

The finite rate of increase (λ) increased with increasing temperatures. It was 1.1153/day at 34.0°C, whereas it was 1.1064/day at 28.0°C. Even though, the **λ** was increased with increasing temperature, a turnaround was noticed in **λ** after 34.0°C and hence at 36.0°C **λ** has been reduced to 1.09804/day (Table 1).

Doubling time (t)

The doublingtime required by BPH to double its population decreased with increasing temperatures. BPH took as long as 6.86 days for doubling the population at 28.0°C, whereas it took only 6.35 days at 34.0°C. However, the decrease in doubling time has a shift after 34.0°C and hence it has been increased to 7.41 days at 36.0°C (Table 1).

Mean generation time (T)

The mean generation time was observed to be decreased with increasing temperatures. The BPH took 35.46 daysto complete the generation at 28.0°C,

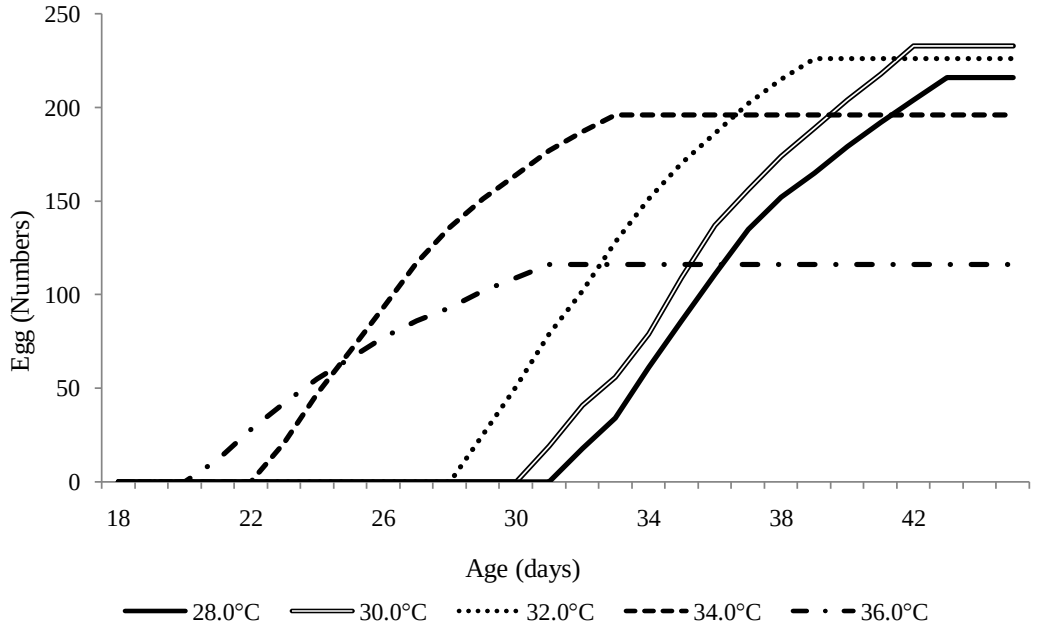

Figure 2. Cumulative fecundity of BPH at different temperature regimes.

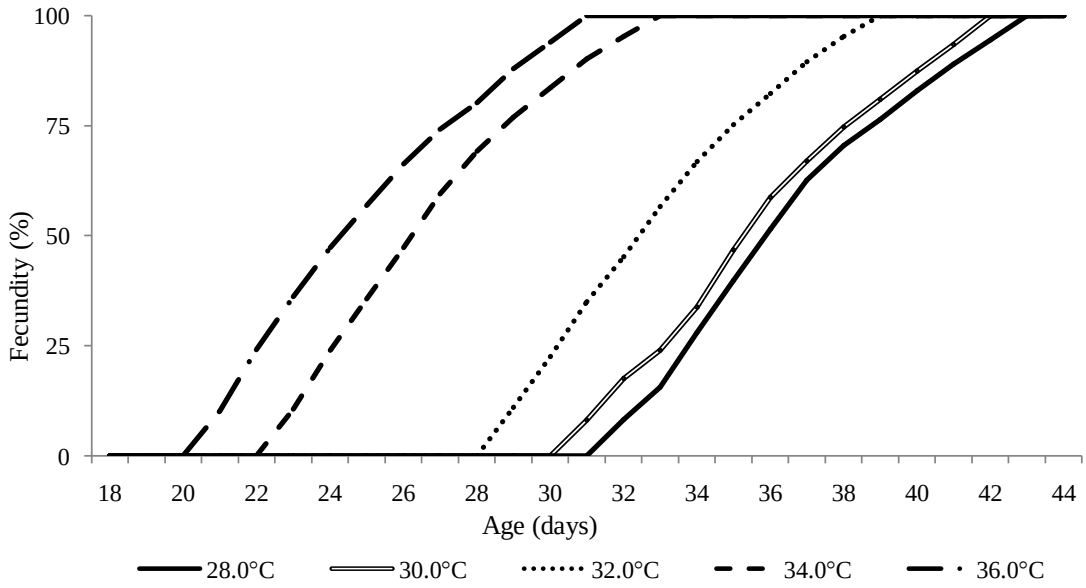

Figure 3. Percent cumulative fecundity of BPH at different temperature regimes.

whereas it took only 23.30 days at 36.0°C (Table 1).

DISCUSSION

Generation time

The mean generation time of BPH was longer at lower temperature regimes and was shorter at higher temperature regimes. Temperature is an important factor, which exerts a profound influence on the development of insects. Development time is mostly dependant on the metabolic rate of the insects. The metabolic rate of insects depends on their body temperature. The temperature inside the insect's body achieves equal or close values to the ambient temperature. Hence, the metabolic rate of insects increases linearly with ambient temperature and results in faster development at higher

temperature (Grodzicki and Walentynowicz, 2011).

Survivorship (l_x)

Survivorship (l_x) decreased with increasing temperature. The time taken for 50% mortality also decreased with increasing temperatures. It indicated that the most of the insects reared under higher temperature regimes died faster and earlier as they were not able to tolerate the higher temperature. When the insects happened to live in higher temperature regimes, respiration increases up to a critical upper limit. After this upper limit, respiration decreases. Hence, higher mortality in insects reared under higher temperature thus explained as the result of decreased respiration when the temperature increased. Yamaguchi et al. (2001) reported that the potential rate of insect population is strongly dependent on temperature, and their survival is impaired at temperature extremes. It was also reported by Kuo et al. (2006) that only 12.5% of nymphs survived when the temperature increased from 10 to 35°C in *T. nigriabdominalis.*

Fecundity

The longer pre-oviposition period at lower temperature may be attributed to the lower metabolic activity at lower temperature regimes (Didonet et al., 1996). Insects need to accumulate more energy to maintain the vital functions. Hence, at lower temperature pre-oviposition period was observed to be more. However, the pre-oviposition period decreased when the insects happened to live at higher temperature regimes as the metabolic rate increased. Similar results were reported by Heong et al. (1995), Son and Lewis (2005) and Ju et al. (2011).

The number of eggs laid by BPH was observed to be lowest at higher temperature regimes. Hence, higher temperature regimes of 34.0 and 36.0°C were not suitable for egg laying and egg growth and development by BPH adults as it reduces fertility and viability of eggs. Xiaoping et al. (1992) also reported that the number of eggs laid by BPH decreased rapidly as the temperature increased.

Net reproductive rate (R_o)

The R_o observed to be decreased at the higher temperature regimes. Similar results were reported by Sataret al. (2008) in cotton aphids. The results revealed that the reproduction rates of the green peach aphid were in general higher at temperatures between 20.0 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 30.0°C. The lowest R_o value at higher temperature could be explained due to the heavy mortality of the immature life stages and also adults between emergence and peak oviposition (Amiri et al., 2010).

Population growth parameters

Intrinsic rate of natural increase, finite rate of increase and doubling time are considered as population growth parameters. Population demographic parameters are important in measurement of population growth capacity of an insect under specified conditions. Iranipour et al. (2003) reported that, developmental time decreased as temperature increased. This is the primary reason why the intrinsic rate of natural increase was observed to increase with temperature in the present study. As pointed out by Lewontin (1965) and Dent and Walton (1997), 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 the eggs are produced; more will be their contribution to the value of r_m (Birch, 1948). Thus, the highest r_m value might be attributed to the earlier oviposition at higher temperature regimes for all the pests. However, the experiment results also revealed that the increase in r_m was not continuous as it reduced at 36.0°C. Similar results were also reported by Kuo et al. (2006), De Conti et al. (2010) and Manikandan et al. (2014). The lowest r_m value at 36.0°C could be explained to the heavy mortality at the highest temperature regime.

Conclusion

The results of the experiments revealed that, population growth parameters are increasing with increasing temperature. However, the increase in population growth parameters had a turnaround at 34.0°C and it started decreasing after 34.0°C. All the growth parameters were observed to decrease at 36.0°C, which reveals that the temperature increase above 34.0°C is detrimental to the development of BPH. If the global warming continuous at the present phase, it will influence the BPH negatively and the population growth would be severely affected in the near future.

Conflict of Interest

The authors have not declared any conflict of interest.

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