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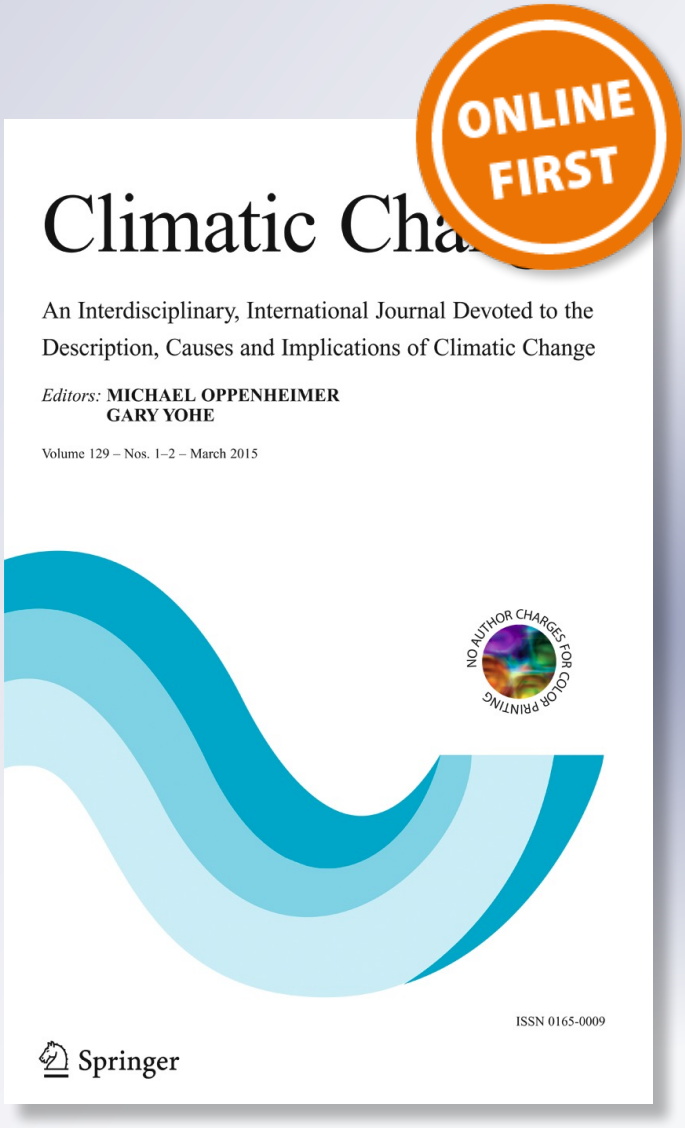

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Simulation of climatic change impact on crop-pest interactions: a case study of rice pink stem borer *Sesamia inferens* (Walker)

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Abstract As climatic change impacts would depend upon complex interactions between climatic and biological factors, crop simulation models would play an important role in predicting such an impact. Present study thus aimed at simulating climatic change impacts on crop-pest interactions through a coupled crop-pest model. Based on temperature-dependent development of pink stem borer, *Sesamia inferens* (Walker) at six constant temperatures viz., 18, 21, 24, 27, 30, 33 and 35±1 °C, thermal constants for eggs, larvae and pupae were determined as 47.6, 700 and 166.7° days, respectively through a linear model with corresponding lower development thresholds being 13.8, 10.6 and 12.7 °C. Besides, optimum temperature and upper developmental threshold, respectively were found to be 34.6 and 36.2 °C for eggs, 34.5 and 36.4 °C for larvae, and 31.7 and 37.0 °C for pupae of the pink stem borer through a non-linear model. Based on the thermal requirements, and biotic and abiotic mortalities, a mechanistic holometabolous population simulation model for *S. inferens* was developed and coupled to InfoCrop-rice model. This coupled InfoCrop model could satisfactorily simulate the PSB dynamics and crop-pest interactions. Validated model was used to simulate the impacts of climatic change on *S. inferens* population and rice crop in accordance with four 'standard special report on emissions scenarios', A1, A2, B1 and B2. Simulations revealed that *S. inferens* population would decline to the extent of 5.82–22.8 % by 2020 and 19.0–42.7 % by 2050 under Delhi conditions. Following decline in pest population, *S. inferens* induced yield losses also revealed a declining trend under changed climate. The coupled crop-pest model can be easily adapted to diverse agro-environments and applied to simulate the pest dynamics and crop losses under location-specific situations.

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1 Introduction

India is the second largest producer and consumer of rice in the world, accounting for 22.3 % of global production. However, rice productivity in India remains poorer than China, Bangladesh and Sri Lanka (Krishnaiah et al. 2008) which could partly be attributed to heavy crop losses inflicted by insect pests. Rice stem borers have been observed to cause 3–95 % yield loss in India (Pathak and Khan 1994). Among the stem borer species, pink stem borer (PSB), *Sesamia inferens* (Walker) is polyphagous and a well-established pest of rice-wheat rotation in the North western plains of India (Singh 2012) and it migrates from paddy to wheat (Kushwaha and Bharti 1994). However, number of pest species associated with different crops and their status are liable to be influenced by climatic change.

In the context of Indian subcontinent, the Intergovernmental Panel on Climate Change (IPCC) has projected that mean air temperature will increase 0.5–1.2 °C by 2020, 0.88–3.16 °C by 2050 and 1.56–5.44 °C by 2080, depending on the pace of future socioeconomic development scenario (IPCC 2007). Climatic change would impacts plant and animal species including insects. Insects will be affected directly through changes in temperature and rainfall patterns and indirectly through their host plants. The impacts on insects may include late onset and early break of dormancy leading to increased period of activity, higher development rates, changes in inter-specific interactions including crop-pest and pest-natural enemy interactions, and altered migration behavior (Root et al. 2003; Parmesan 2006; Sujithra and Chander 2013). It thus becomes pertinent to assess climatic change impacts on important crop pests to be able to gauge their effect on agricultural productivity.

In general, effects of rice stem borers on rice yield have been quantified empirically by yield-infestation regression models, but do not take into consideration the physiological basis of pest damage. Consequently, these relationships are location-specific and cannot be extrapolated without risk of error (Pinnschmidt et al. 1995). On the other hand, crop simulation models based on detailed eco-physiological crop processes and pest damage mechanisms take in to consideration plant physiological processes affected by pest injury. These models are universal in approach and can account for variability in weather, soil, crop management practices and pest situations encountered at different locations (Chander et al. 2007). Simulation models have been widely used to predict climatic change impact on crops, however, crop pests have largely been ignored in such studies (Teng et al. 1996).

Potential damage mechanisms have been identified that link the pest effects to crop growth and development at the physiological level (Rabbinge et al. 1989). Population dynamics models linked to crop growth models could simulate pest population peaks; estimate timing of spray schedules based on economic thresholds; optimize pest management strategies (Kropff et al. 1995; Teng et al. 1996; Sutherst et al. 2011) and assess climatic change impacts on pest dynamics (Benigno et al. 1988). We developed a generic crop simulation model InfoCrop for tropical environments (Aggarwal et al. 2006) that was coupled with several pest damage mechanisms and used for assessing crop loss and developing decision support tools (Sujithra et al. 2011). However, InfoCrop lacked an insect dynamics simulation module and crop loss simulation needed input of pest population/damage. This necessitated the development of an insect dynamics simulation module for its coupling with InfoCrop. Understanding of thermal requirements of the insect species is essential and its use instead of their developmental period in mechanistic population dynamics model enhances their predictive value. Kiritani (1988) urged the use of these for insects in predicting the phenology of insect communities under global warming. The present study was undertaken to develop a

mechanistic population simulation model of *S. inferens* and couple it with InfoCrop model to facilitate assessment of climatic change impacts on the pest dynamics and crop-pest interactions in rice. Such a model can be easily adapted to weather conditions, crop management practices and pest situations encountered in diverse agro-ecologies and applied to simulate the pest dynamics and crop-pest interactions under location-specific situations.

2 Materials and methods

2.1 Temperature-dependent developmental stages of *S. inferens*

Culture of *S. inferens* was established through its field-collected larvae in a laboratory at 25± 1 °C and 60–70 % relative humidity (RH) at the Indian Agricultural Research Institute (IARI), New Delhi, India. The pest larvae were further maintained on maize plants as per Easwaramoorthy and Shanmugasundaram (1988) until pupation. The moths were fed with 10 % sucrose solution soaked in cotton wool and 40–50 day old maize plants were offered to them for oviposition in a mylar cage. The egg masses were collected by cutting off the leaf section and then used to study temperature-dependent development of the pest.

Development of *S. inferens* was studied under 18, 21, 24, 27, 30, 33 and 35±1 °C with 65–70 % RH in biological oxygen demand (BOD) incubators. Eggs were kept for hatching in test tubes in batches of 20 eggs in three replicates at each of the temperatures. Following hatch, first instars were transferred to maize plants, covered with a mylar film cage, and reared in replicates of 20. Observations of egg hatch, larval duration, pupal duration and adult emergence were made at 24-h intervals. Incubation period and instar stage development duration were determined at each of the temperatures. Temperature-dependent development was inclusive of insect mortality/survival. Individuals that failed to complete a development stage were not included in data computation. Fecundity of the pest was observed at three temperatures, 21±1, 25±1 and 29±1 °C by releasing a freshly emerged pair of adults in five replicates. Newly emerged adults were assigned to sexes to determine sex ratio.

2.2 Thresholds and thermal constant for *S. inferens* developmental stages

Five larval instars of the *S. inferens* were clubbed into two groups, the first three into one and the last two into another, henceforth called small larvae (SLV) and large larvae (LLV), respectively. Being a borer pest, observations on individual larval instars would have required too frequent splitting open of plants, thereby disrupting normal larval development. The larval instars were thus clubbed in to two groups. Development rates of egg, SLV, LLV, and pupae were computed as the reciprocal of their respective developmental duration (D) such that R = 1/D. Lower development threshold (T_0) and thermal constant (K) were then determined by regressing development rate on temperature (Kipyatkov and Lopatina 2010). According to the rule of thermal summation:

$$(T - T_0) \times D = K \quad (1)$$

where T = temperature at which insect species is reared, K = reciprocal of the regression coefficient (b) computed between development rate and temperature:

$$K = 1/b \quad (2)$$

and T_0 = ratio of regression intercept (a) and b:

$$T_0 = -a/b \tag{3}$$

Upper development thresholds (T_m) of different developmental stages of the PSB were computed by the non-linear Lactin 2 Model (Lactin et al. 1995).

$$1/D = e^{\rho^* T} - e^{[\rho^* Tmax - (Tmax - T)/\Delta T]} + \lambda \tag{4}$$

SPSS 16.0 software was used to estimate parameters of Lactin model following Leverberg-Marquardt method. Optimum temperature (Topt) for development of the PSB was calculated according to Logan et al. (1976).

$$Topt = Tmax(1 + \varepsilon^* \ln(\varepsilon^* bo)/(1 - \varepsilon * bo)) \tag{5}$$

where, $\varepsilon = \Delta T/Tmax$ and $bo = \rho * Tmax$.

However, corresponding values of thermal constant, lower developmental threshold, upper developmental threshold and optimum temperature for small larvae and large larvae were pooled to compute a single value of each parameter for complete larval development of the PSB, that was subsequently used in population simulation model.

2.3 Development of population dynamics simulation model for *S. inferens*

A holometabolous population simulation model for *S. inferens* was formulated based on different bio-ecological parameters such as fecundity, sex ratio, adult longevity, biotic and abiotic mortality factors, thresholds of development and thermal constants of different development stages. Information on biotic mortality factors such as egg parasitism and also on sex ratio of the pest (Joshi et al. 2009a; Reddy 2001) was collected from literature resources. On the other hand, information on fecundity, egg infertility, sex ratio, adult longevity and abiotic mortality factors such as temperature-dependent mortality was generated in present study. The model was written in 'Fortran Simulator Translator' Windows version 1.06 (Rappoldt and Van Kraalingen 1996). The continuous dynamic simulation model follows the 'state- rate variable approach'. Numbers of eggs, larvae, pupae, and adults at any given time are the state variables, while their corresponding rates of change represent the rate variables. The model comprised of four developmental stages of *S. inferens*, egg, larva, pupa, and adult. Delay functions were introduced for egg, larval, pupal, and adult stages to ensure that these stages did not appear before fulfillment of their respective thermal requirements. The dynamic section of the model contained various rate and state variable calculations. State variables i.e. total number of eggs, larvae, pupae and adults were calculated on daily based their corresponding initial values and rates of change (equation 6–9 supplementary file).

Rate of change in number of different development stages depended on their respective formation rates, loss rates and rates of conversion to subsequent stage (equation 10–13). The rate of oviposition depended upon adult number, sex ratio and fecundity (equation 14). Fecundity was linked to temperature, and average temperature 25±1 °C was deemed to be optimum for it as a female on an average laid 332±6.69 eggs, however, which was dropped to 245±5.29 and 216±8.29 eggs/female at 21±1 °C and 29±1 °C, respectively. The sex ratio of the PSB was taken as 1:1 as observed in the present study and also reported earlier (Reddy 2001). Rate of formation of larvae, pupae,

and adults depended upon number of eggs, larvae and pupae, respectively and ratio of corresponding daily effective temperature and thermal constant of different stages (equation 15–17). Egg loss rate was calculated from egg production rate and egg mortality (equation 18).

The egg mortality was comprised of biotic and abiotic mortality factors such as egg infertility, egg parasitism, egg predation, and adverse effect of high or low temperature on egg survival. Based on lower developmental threshold, optimum temperature and upper temperature threshold determined for the PSB in the present study, an average temperature from 18.8–29.6, 15.6–29.6 and 17.7–26.7 °C was considered as favourable range for the survival of eggs, larvae, and pupae, respectively (Andreadis et al. 2013). On the basis of temperature-dependent survival of the PSB stages (Table 1), 3.3–15.0 % egg mortality, 6.9–13.7 % larval mortality, and 5.8–11.2 % pupal mortality was incorporated in the population model in a temperature-dependent manner. A value of 62 % egg parasitism was used (Reddy 2001; Joshi et al. 2009a). On either side of the favorable temperature ranges, the survival of different developmental stages was reduced. Egg infertility was used as a parameter in the model and its average value was derived as 9.2 % based on our observations on temperature-dependent hatching of the PSB eggs (Table 1) (equation 19).

The larval loss rate depended upon larval formation rate and their mortality rate (equation 20). The larval mortality rate comprised of larvae parasitism, predation, and adverse effect of temperature on survival (equation 21). The pupal loss rate depended upon pupal formation rate and their mortality rate (equation 22). The pupal mortality rate comprised of pupal parasitism, predation and adverse effect of temperature on survival (equation 23). Published information on parasitism and predation of larvae and pupae was not available, and their values were set to zero in the model. The adult mortality constituted of natural adult death and death due to physical factors (equation 24). Adult PSB died in proportion to the ratio of their daily effective temperature and thermal constant. An average adult mortality due to physical factors value of 4.8 % was used based on temperature-dependent adult survival.

Effective temperature values for eggs, larvae, pupae, and adults were determined based on daily average temperature and their respective lower development thresholds (equation 25). The effect of global warming was introduced as an increase in both maximum and minimum temperatures (equation 26–27).

Table 1 Effect of temperature on development of various stages of *S. inferens*

Temperature (°C)	Duration of different stages of *S. inferens* (days)				Total developmental period (days)
	Egg incubation period	Small larvae	Large larvae	Pupae	
18±1	10.50±0.496	31.44±0.765	26.09±0.090	48.59±0.696	116.62
21±1	6.50±0.496	23.16±0.601	20.88±0.111	18.10±0.099	68.64
24±1	4.50±0.496	22.80±0.583	15.5±0.956	13.93±0.066	56.73
27±1	3.50±0.496	18.00±0.577	11.30±0.517	9.33±0.188	42.13
30±1	3.00±0.00	15.00±0.577	10.40±0.518	8.33±0.188	36.73
33±1	2.00±0.00	12.5±0.500	9.36±0.677	7.91±0.083	31.80
35±1	2.70±0.00	13.7±0.553	9.90±0.789	8.10±0.102	34.40

2.4 Validation of pink stem borer population simulation model

The population simulation model of the PSB was validated using field experiment data (Joshi et al. 2009a) that was acquired during the rainy season in 2004. The population model was initialized with a number of adults that would oviposit a number of eggs equal to those observed in the field experiment. The pest population was simulated under the same biotic mortality factors and weather as in the field experiment. The simulated and observed population of different developmental stages of the PSB were analyzed through simple linear regression and compared by root mean square error.

2.5 Coupling of population dynamics model with InfoCrop model

InfoCrop-rice, a crop growth model could be used to simulate PSB damage on rice. However, simulation of pest damage required pest population as an input because the model did not simulate the pest dynamics. To accomplish this, InfoCrop-rice was coupled to a PSB population model. In the coupled model, daily PSB damage depended on number of larvae generated by the population model and larval feeding rate. It was computed as 1.69×10^{-4} kg/larva/day, based on dry weight of a rice stem (1.69×10^{-3} kg) that was damaged by one larva over a 10-day period, thus creating a whitehead. Larval feeding rate was subsequently calibrated to be 1.75×10^{-4} kg/larva/day, using replicated experimental data on crop yield that was obtained by releasing 1, 2, 3, 4, 5 and 6 larvae/4 rice hills in the field. The PSB damage resulted in loss of leaf area as well as loss of weights of different plant organs. The effect of the PSB damage on crop leaf area and plant organ dry weight was simulated by reducing them in proportion to the ratio of daily PSB damage and total stem weight of the crop (equation 28). Effect on leaf area (equation 29–30), leaf weight (equation 31–32), stem weight (equation 33–34), stem area (equation 35), storage organs (equation 36–37), available nitrogen in the plant, nitrogen loss in plants due to the PSB damage (equation 38–39) were simulated in the model.

Performance of the population model of the PSB was compared with observed data on number of eggs, larvae, and pupae of the PSB (Joshi et al. 2009b). The model was validated for crop-pest interactions using data of two field experiments that were conducted to assess yield loss under different larval densities of the PSB during the 2009 and 2010 rainy seasons (Selvaraj and Chander 2012). The experiments comprised of releasing 1, 2, 3, 4, 5 and 6 larvae / 4 rice hills during reproductive crop stage and measuring their effect on crop yield. The population model was initialized with a 800, 1600, 2400, 3200, 4000 and 4800 adults/ha that generated respective larval density of 1, 2, 3, 4, 5 and 6 larvae/ 4 hills which was caused around 2, 5, 10, 15, 20 and 25 % PSB damage, respectively. The PSB damage was thus simulated under each of the specified larval densities. Observed and simulated larval populations and yields were compared.

2.6 Climatic change impacts on *S. inferens* dynamics and crop-pest interactions in rice

Impact of climatic change on the PSB population and crop-pest interactions was studied through the coupled InfoCrop-rice model. The model was run with ambient temperature under 390 ppm CO_2 and with a 0.5, 1.0 and 1.5 °C average temperature increased at 410 ppm CO_2, and with a 2.0, 2.5 and 3.0 °C average temperature increased at 450 ppm CO_2 from the 2001 to 2010 rainy seasons under New Delhi conditions. These combinations of CO_2 and increased

temperature represented all probable predictions across the four standard SRES socio-economic scenarios, A1, A2, B1 and B2 that have been projected under climatic change for the Indian sub-continent through CCSR/NIES coupled A-OGCM (Lal et al. 2001). The PSB population as well as crop yield was recorded at ambient temperature as well as each of the increased temperatures during all the years. Simulated pest population and crop yield trends were interpreted and reasons for pest population change were also explored.

3 Results

3.1 Thresholds and thermal constant for different developmental stages of *S. inferens*

Temperature increase from 18±1° to 33±1 °C reduced incubation period and duration of different developmental stages of the PSB (Table 1). None of the PSB life stages could develop below 10 °C or above 39 °C. Consequently, total development duration of the PSB decreased from 116.6 at 18±1 °C to 31.8 days at 33±1 °C. Incubation period and developmental duration of the developmental stages at 35 and 30 °C were found to be greater than at 33 °C, indicating the occurrence of optimum temperature for the pest between 33 and 35 °C. Egg hatch, larval survival, pupation and adult survival also slightly decreased with increase in temperature from 18±1 to 33±1 °C. The lower developmental thresholds were determined to be 13.8, 10.0, 11.2 and 12.7 °C for eggs, small larvae, large larvae, and pupae with the corresponding thermal constant of 47.6, 500.0, 200.0 and 166.7° days (DD), respectively (Table 2). Likewise, the respective upper developmental threshold and optimum temperature were 36.2 and 34.6 °C for egg stage, 36.6 and 34.6 °C for SLV, 36.1 and 34.4 °C for LLV, and 37.0 and 31.7 °C for pupal stage (Table 3). Total thermal requirement from oviposition to adult emergence was found to be 914.3 DD. Thermal constant, lower and developmental threshold and optimum temperature for complete larval development, respectively, were 700 DD, 10.6, 36.4 and 34.5 °C.

3.2 Model validation

The number of eggs, larvae, and pupae of the PSB, simulated under experimental conditions as in Joshi et al. (2009b), were proximal to the observed number of these development stages (R^2 = 0.99, RMSE = 5.66 %). Likewise, simulated and observed yield under different larval densities was very close (R^2 = 0.97; RSME = 6.89 %). This coupled InfoCrop model could satisfactorily simulate the PSB dynamics and crop-pest interactions in rice.

3.3 Impact of climatic change on *S. inferens* population dynamics

As CO_2 did not directly affect pest development (Yin et al. 2010), the PSB population was thus influenced only by temperature rise. The 0.5–1 °C average temperature increased over 2001–2010 rainy seasons showed a slight decrease in the number of the PSB developmental stages (Fig. 1a). However, 1.5–3.0 °C average temperature increase resulted in 10.8–38.9, 30.1–60.4, 31.2–56.4 and 24.6–52.7 % decline in egg, larval, pupal, and adult population of *S. inferens*, respectively (Fig. 1a) due to reduction in its fecundity and survival with increased temperature (Fig. 2a, b). The magnitude of the PSB population decline increased with temperature increased. The pest fecundity consistently decrease from 81.4 eggs/female/day at ambient

Table 2 Threshold temperatures and thermal constant for different developmental stages of *S. inferens*

Stem stem borer developmental stage	Regression equation	Thermal constant (K) (K = 1/b)	Temperature threshold (T_0) (T_0 = a/b)	R^2
Egg	Y = 0.021X-0.290	47.6	13.8	0.94
Small larva	Y = 0.002X-0.020	500.0	10.0	0.92
Large larva	Y = 0.005X-0.056	200.0	11.2	0.76
Pupa	Y = 0.006X-0.076	166.6	12.6	0.89

temperature to 43.3 eggs/female /day with 3 °C temperature rise (Fig. 2a). Likewise, survival of the PSB stages was adversely affected by temperature increased. Egg mortality increased from 73 % at ambient to more than 90 % with a 2–3 °C temperature increased (Fig. 2b). The survival of other development stages was also similarly affected by temperature increased. Up to 1.5 °C temperature increase did not show any effect on total duration of the PSB (54.3 days), but with a 2–3 °C increase it increased to 55.8 days. In view of climatic change projections for the Indian sub-continent, the PSB population would decline 5.8–22.8 % by 2020 (0.87–1.17 °C increase) and 19.0–42.7 % by 2050 (1.81–2.37 °C increase) under Delhi conditions (Fig. 3).

3.4 Impact of climatic change on crop-pest interactions

With a 0.5–1.5 °C temperature increase at 410 ppm CO_2, yield of an uninfested crop ranged from 4262 to 4690 kg/ha, while it was 3574–4131 kg/ha under a 2–3 °C temperature increase at 450 ppm CO_2 compared to 4905 kg/ha at ambient temperature and CO_2. The yield of an uninfested crop thus declined with increased temperature compared to ambient conditions, indicating that climatic change might adversely affect rice yield even without pest infestation (Fig. 4a). The greater the temperature increase, the greater was the decline in crop yield. With a 0.5–1.5 °C temperature increase, the yield of an infested crop ranged from 3749 to 3944 kg/ha, while with a 2–3 °C temperature increase it varied from 3397 to 3729 kg/ha, compared to 3953 kg/ha at ambient conditions. In accordance with a decline in the PSB population, yield loss due to the pest showed a declining trend with intensity of climatic change from 19.41 % at ambient to 4.98 % with 3 °C average temperature increase under New Delhi conditions (Fig. 4b).

Table 3 Parameters of the Lactin 2 non-linear model for development of *S. inferens*

Developmental stage	P*	ΔT	λ	Topt	Tmax	R^2
Egg	0.017	0.095	−1.264	34.6	36.2	0.966
Small larva (1–3 instar)	0.003	0.129	−1.022	34.6	36.6	0.971
Large larva (3–5 instar)	0.003	0.241	−1.022	34.4	36.1	0.971
Pupa	0.006	0.565	−1.089	31.7	37.0	0.956
Total development	0.001	0.193	−1.071	34.4	36.0	0.994

*ρ= Composite value for critical enzyme catalyzed biochemical reactions, ΔT= temperature range above the optimum temperature for development and below Tmax, λ= Directly measurable rate of temperature dependent physiological process at a base temperature, Topt-= Optimum temperature for development of the pink stem borer and Tmax- upper developmental threshold

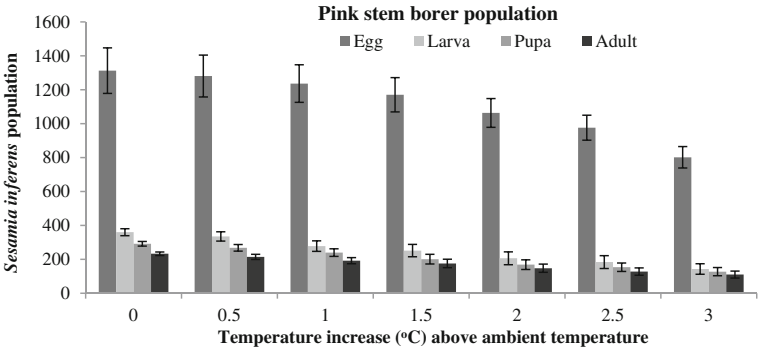

Fig. 1 Effect of global warming on population of different life stages of *S. inferens* at New Delhi conditions

4 Discussion

In the present study, temperature-dependent development of the PSB over a range of constant temperatures from 18±1 to 33±1 °C followed a linear relationship and facilitated quantification of stage-specific thermal constants and lower development thresholds of the pest. However, greater duration of all the PSB stages at 35 °C compared to 33 °C, suggested that the

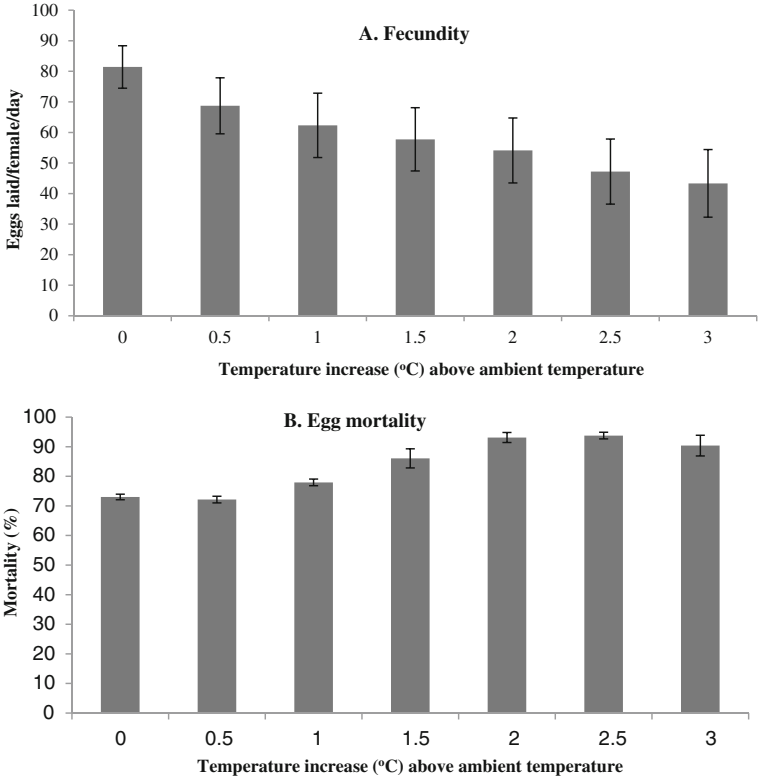

Fig. 2 Effect of temperature rise on (**a**) fecundity and (**b**) mortality of *S. inferens* at New Delhi conditions

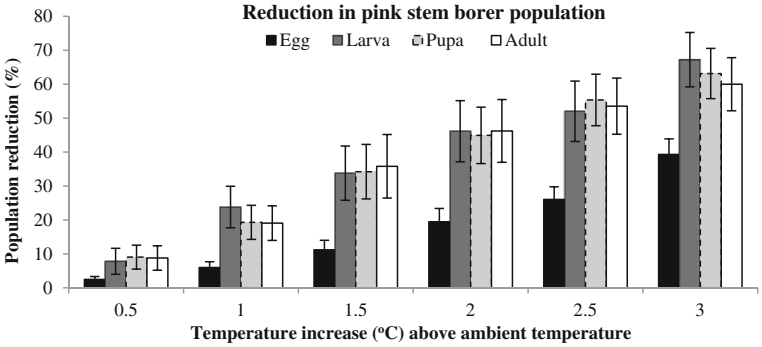

Fig. 3 Impact of global warming on population reduction of different life stages of *S. inferens* at New Delhi conditions

relationship between the pest development and temperature was not linear. As the linear model could not determine upper developmental thresholds and optimum temperatures these were computed through a non-linear model (Lactin et al. 1995). This model is an improved version of Logan et al. (1976) and it relates insect development rate to enzyme activity. The linear relationship between development rate of the PSB and temperature within 18 to 33 °C has also been reported earlier (Rahman and Khalequzzaman 2004). Optimum temperature for eggs and larvae was similar (34.4 to 34.6 °C), while it was 31.7 °C for pupae. Optimum temperature for

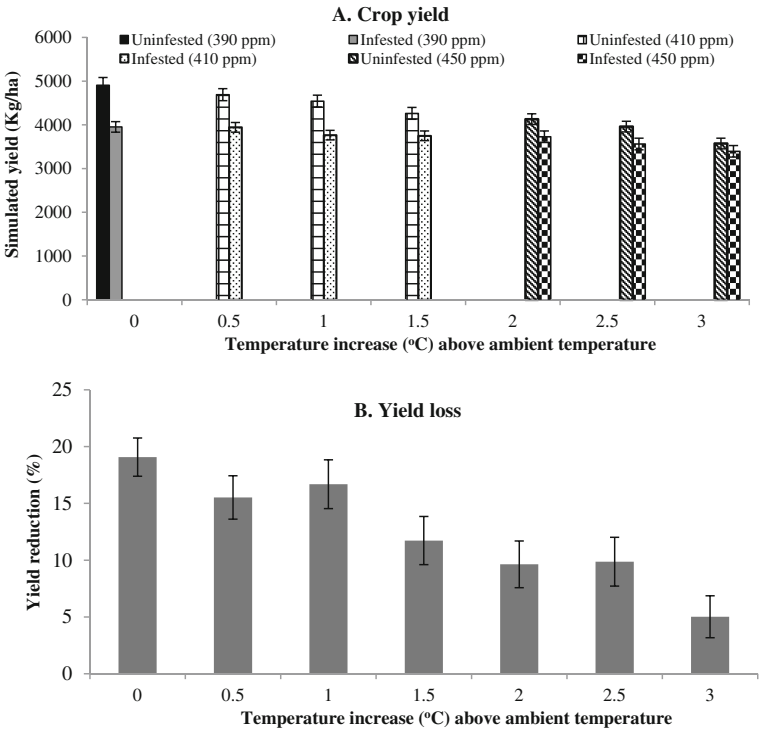

Fig. 4 Effect of climatic change (CO_2 and temperature) on (**a**) and (**b**) yield reduction of uninfested and *S. inferens* infested crop at New Delhi

different developmental stages characterized upper limits of the linear relationship between development duration and temperature. A lower optimum temperature for the pupal stage compared to egg and larval stages suggested a higher sensitivity to temperature because of pupa being in a transformational stage in the insect life cycle. Based on lower developmental threshold and optimum temperature, the favourable range of temperature was, 13.8 to 34.6 °C for eggs, 10.6 to 34.5 °C for larvae, and 12.7 to 31.7 °C for pupae. The results were accordance with Andreadis et al. (2013); Orang et al. (2014). Development duration for the pupal stage at 30 and 33 °C only marginally differed compared to the difference in development durations of egg or larval stages at these temperatures. The upper developmental threshold for different developmental stages of the PSB ranged between 36.1 and 37.0 °C, indicating the maximum temperature at which life processes could no longer be maintained (Logan et al. 1976) and consequently the pest development ceased to occur.

Thermal constant and lower development threshold of the PSB stages were computed according to Kipyatkov and Lopatina (2010), which single values of these parameters for a particular development stage of the PSB unlike another method (Uvarov 1931). A thermal constant value as 914.3 DD for egg to adult emergence of the PSB in our study was higher than 838.0 DD reported earlier (Rahman and Khalequzzaman 2004), probably owing to experimental variability in the two studies. As a matter of fact, the thermal constant, being an amount of heat energy required for completion of a particular life stage or complete life cycle of an insect species, should not have any spatio-temporal variation. Owing to this property of stability, thermal constant has been found to be useful for forewarning and monitoring of insect populations, and timing of insecticide applications (Messenger 1958; Zalom et al. 1983).

An average temperature from 18.8–29.6, 15.6–29.6 and 17.7–26.7 °C was considered as a favourable range for eggs, larvae, and pupae of the PSB, respectively. Average temperature was used instead of daily maximum and minimum temperatures because the thermal constant computation is also based on average temperature and all computing in InfoCrop model is also based on average temperature. In InfoCrop, non-linear relationship between development of the PSB stages and temperature was accounted for by reducing development rate on either side of the favourable temperature range. In terms of daily maximum and minimum temperature under field conditions in Delhi, the aforementioned average temperature ranges were commensurate to 13.8–34.6 °C for eggs, 10.6–34.6 °C for larvae, and 12.7–31.7 °C for pupae of the PSB. For example, in the case of average temperature from 18.8 to 29.6 °C for eggs of the PSB, the upper limit of 24.1 °C would be the result of a maximum of 34.6 °C and a minimum of 24.6 °C. Likewise, an average of 18.8 °C would be due to a maximum of 23.8 °C and a minimum of 13.8 °C; given a general difference of approximately 10 °C between maximum and minimum temperature during the rainy season at Delhi.

One generation of the PSB was completed in 53–58 days during years with different ambient temperature. Simulated populations and generation time differed across years due to weather variability. As soon as the thermal constant requirement of a developmental stage was fulfilled, it transformed into the next stage subject to stage specific mortalities. Among physical factors, extreme temperature affected the PSB population through reduced survival as well as reduced development rate. Among biotic mortality factors, egg infertility and egg parasitism (Reddy 2001) also reduced the pest population depending upon their intensity. The PSB population dynamics module facilitated simulation of crop-pest interactions for a specified time period during which the pest was observed in the field. It has been reported

previously that dynamic, physiologically-based pest-crop models allow simulation of yield losses in a real-time pest-crop system and that the approach has the potential to be applied across pest situations and cropping conditions (Kropff et al. 1995). Earlier, the InfoCrop-rice model coupled with a hemimetabolous population simulation model could assess climatic change impacts on brown planthopper population and rice yield under different agro-ecological environments (Sujithra and Chander 2013).

The model predicted that a 1 °C average temperature increase at New Delhi would not significantly affect the PSB population but further temperature increase would adversely affect the population. Temperature increase beyond 1.5 °C was found to adversely affect the pest population due to reduction in its fecundity and survival. The lower developmental thresholds of the PSB developmental stages in our studies ranged from between 10 and 13.8 °C, while the optimum temperatures and upper development thresholds ranged from 31.7–34.6 and 36.1–37.0 °C, respectively. The present study results were in close agreement with Andreadis et al. (2013); Orang et al. (2014). The present study thus implied that the development rate of the PSB stages would increase between the lower development thresholds and optimum temperature with an increase in the ambient temperature, which however would decline beyond the optimum temperatures until the upper thresholds. With more than a 1 °C average temperature increase, ambient temperatures at New Delhi and other similar environments might exceed the favourable temperature range for the PSB, thereby adversely affecting its development rate, survival and fecundity. Given the 0.87–1.17 and 1.81–2.37 °C temperature rise by 2020 and 2050, respectively, the PSB population was thus predicted to have greater reduction (19.0–42.7 %) by 2050 than by 2020 (5.8–22.8 %) compared to 2001–2010 weather in Delhi. As ambient conditions differ in different agro-ecological regions, the climatic change impact on the PSB is likely to differ among agro-climatic regions. It has been observed that insects in warmer climates were already surviving at upper limits of their favourable temperature range and any increase in temperature would adversely affect their growth and development (Bale and Hayward 2010). Diverse effects of changed temperature in diverse ecosystems have been reported in the case of rice brown planthopper (Heong et al. 1995; Sujithra and Chander 2013). Reji and Chander (2008) analyzed impacts of global warming on rice bug (*Leptocorisa acuta)* that predicted an adverse effect of more than 1 °C temperature rise on the bug under Delhi environment. Concomitant to a decline in the PSB population, pest-induced yield losses in rice depicted a declining trend with increased temperature in our study. However, rice productivity also declined under climatic change even without pest stress. This results conformed the earlier report (Auffhammer et al. 2011). The coupled model could predict probable changes in rice yield and yield losses caused by the PSB under different climatic change scenarios. The PSB population simulation model coupled to InfoCrop-rice model thus facilitated assessment of climatic change climatic on the pest dynamics as well as crop-pest interactions in rice. The coupled InfoCrop-rice model can easily be adapted to diverse agro-ecologies and used for location-specific applications related to climatic change impacts and pest forewarning. Such studies also need to be undertaken for other important pests of different crops.

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