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# Thermal Stress: A Major Influencing Factor on Development of *Phenacoccus solenopsis* and *Paracoccus marginatus* Infesting Major Crops - A Review

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## Abstract

The cotton mealybug and papaya mealybugs are major invasive pests damaging economically important agricultural and horticultural crops. Changes in environmental conditions leads to severe outbreaks and may cause extensive damage to the crops. Recently, thermal stress-related researches on mealybugs were typically conducted at a range of constant temperatures. Hence basic knowledge on developmental biology of mealybugs, biochemical changes and expression of heat shock protein under stress condition is important. The above information will be useful for predicting the population dynamics and to develop a potential to develop a mealybugs under variable environments. The review reveals the basic information about mealybugs pests, status of occurrence, symptoms of damage, developmental biology of mealybugs under different temperatures, regimes, oxidative stress enzymes level and different heat shock proteins expressed under thermal stress condition. Our preliminary studies revealed that the temperature above 34 °C negatively influences the growth and development of both the mealybugs. Similarly continuous exposure to extreme temperature (< 40 °C) significantly affected the survival and development of the mealybugs

## Introduction

Mealybugs are the major menace in recent years in major agricultural and horticultural crops. Among the mealybugs, *Paracoccus marginatus* Williams and Granara De Willink (infesting more than 40 agricultural and horticultural crops), *Phenacoccus solenopsis* (a major pest of cotton in India and Pakistan in over 2 million ha) and *Maconellicoccus hirsutus* (pest of > 20 crops) warrants novel and sustainable pest management interventions. Beside these mealybugs, more recently there are other mealybug species *viz*., *Nipaecoccus viridis,* and *Rastrococcus iceryoides* found to cause serious damage to various agricultural and horticultural crops. Mealybugs feeds on phloem tissue, removing plant sap and causing the leaves to distort, yellow and even drop and severely affected plants may die. Management strategies are less effective as it inhabits concealed locations and even in exposed conditions, the congregation of individuals, protection of late age nymphs and adults by loose, cottony waxy substance secreted by mealybugs and oviposition in waxy pouches act as barriers to proper penetration and action of insecticides. In recent years, the occurrence of Solenapsis mealybug *P. solenopsis* at varying levels of severity on cotton brinjal and tomato was reported by several authors (Rishi Kumar, 2013; Vennila and Agarwal, 2013). and the papaya mealybug, *P. marginatus* a native of Mexico, invaded several countries including India, Srilanka and other South East Asian countries was first reported from Coimbatore in July 2008 (Muniappan *et al.,* 2008) and subsequently found causing extensive damage to papaya plantations across the country (Mani *et al.,* 2012; Sharma, 2013).

The ability of an insect to develop at different temperatures is an important adaptation to survive under various climatic

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conditions (tropical, subtropical, and temperate), which will help in predicting the insect outbreaks (Mizell and Nebeker, 1978). The rate of insect development is affected by temperature to which the insects are exposed (Campbell *et al.,* 1974). Insects require a certain amount of heat units (degree-days) to develop from one life stage to the next (Gordan, 1999). The potential rate of increase of any insects is strongly dependent on temperature, and their survival is impaired at temperature extremes. The effect of high-temperatures on lifetime reproductive success of animals depends on the corresponding effects on physiological constraints. Insects are ectotherms; their body temperature varies with the outside environment. In ectotherms, increase in temperature positively correlation with increased metabolic-rate, which in turn affect the reproductive success.

In general, mealybugs, regulate their body temperature which must be balanced between the rate of heat gain from metabolism and external source, and the rate of heat loss to environment (Casey, 1992). Heat transfer is an important physical process to gain and loss heat in insects by four mechanisms: radiation, conduction, convection, and evaporation (Norris and Kunz, 2012). Several factors such as body size, shape, surface area, coloration will affect capacity to maintain the body temperatures of the insects (Pereboom and Biesmeijer, 2003). For example, nymphs are considered more sensitive to environmental conditions than adults because nymphs with smaller body size will reach equilibrium state quicker than adults (Stevenson, 1985; Piyaphongkul *et al.,* 2012). Since temperature is the main abiotic factor affecting development, the understanding of the physiological relationship between temperature and development rate is an important criterion for the prediction of population outbreaks and timely management of pests on crops (Jervis and Copland, 1996; van der Have, 2008). Mealybugs are soft bodied insects and they vulnerable to climate change. Because of their small size their basic physiological functions are strongly influenced by environmental temperature. The developmental biology of *P. solenopsis* and *P. marginatus* may vary according to the host plant and other abiotic factors particularly temperature. A better understanding of the biology and temperature requirements of this pest will help in identify the population dynamics and to formulate the management strategy.

## Effect of Thermal Stress on Biology and Development of *P. solenopsis*

The mealybug, *P. solenopsis* has a wide geographical distribution with its origin in Central America (Fuchs *et al.,* 1991). It has been described as a serious invasive pest in India, Pakistan (Hodgson *et al.,* 2008), China (Wang *et al.,* 2009), Nigeria (Akintola and Ande, 2008) and in Sri Lanka (Prishanthini and Laxmi, 2009) on cotton and other crops. The occurrence was first reported in cotton in Pakistan and India during 2004 (Ping *et al.,* 2010). The, severe incidence of *P. solenopsis* was noticed in later phase of cotton (Rishi Kumar, 2013) and tomato (Vennila and Agarwal, 2013).

The reproductive potential of the *P. solenopsis* population is very great at suitable temperature, making it easy to outbreak. The intrinsic rate of increase of *P. solenopsis* was highest at 35 °C in combination with 65% RH. Chen *et al.*, (2015) reported that, temperature, RH and their interactions significantly influenced the life history traits of *P. solenopsis.* First instar was the most sensitive stage to extreme temperatures with very low survival rates at 15 and 35 °C. At 25-32.5 °C and the three RHs, the developmental periods of entire immature stage were shorter with values between 12.5-18.6 d. The minimum threshold temperature and the effective accumulative temperature for the pest to complete one generation were 13.2 °C and 393.7 degree-days, respectively. The percentage and longevity of female adults significantly differed among different treatments. It failed to complete development at 15 or 35 °C and the three RHs. Female fecundity reached the maximum value at 27.5 °C and 45% RH. The intrinsic rate for increase (r), the net reproductive rate ($R_0$), and the finite rate of increase (k) reached the maximum values at 27 °C and 45% RH (0.22 d1, 244.6 hatched eggs, and 1.25 d1, respectively). Therefore, we conclude that 27.5 °C and 45% RH are the optimum conditions for the population development of the pest.

Prasad *et al.* (2012) the development duration of female and male nymphal instars linearly decreased with the increase in temperature from 18 to 32 °C and cumulative developmental time of females ranged from 43.9 d for 18 °C to 15.0 d for 32 °C (Prasad *et al.,* 2012). According to Sanjeev Kumar *et al.* (2013), nymphal duration had a linear decrease with increase in temperature from 20 to 35 °C and it was in the range 16.4 days (20 °C) to 20.2 days (35 °C). Below 53 percent of survival of crawlers to adult was reported as lowest which has been recorded at 20 and 36 °C and highest of 80 percent was evident at 32 °C.

## Effect of Thermal Stress on Biology ond Development of *P. marginatus*

The papaya mealybug, *P. marginatus* is native of Mexico invaded several countries including India (Muniappan *et al.,* 2008). Thangamalar *et al.* (2007) described *P. marginatus* as an invasive pest from Central American countries. This mealybug caused havoc in agricultural and horticultural crops in India ever since its first report from Coimbatore during 2007. Within three months of its first report of occurrence of *P. marginatus* in Indonesia spread across the South East Asian countries in pandemic proportions (Muniappan *et al.,* 2008). This mealybug posed a great threat to commercial papaya plantations in Sri Lanka spanning approximately 6,200 ha was later spread to India (Anonymous, 2009) and in Bangladesh it caused immense damage to the field crops, vegetables and ornamental plants of economic importance (Helal *et al.,* 2012).

Recent years, the incidence of this pest at varying level of intensity was noticed in cotton, brinjal other vegetables and papaya (Mani *et al.,* 2012; Sharma, 2013). Tanwar *et al.* (2010) worked on the incidence and damaging value of papaya mealybug and its management strategies. These mealybugs are most active in warm and temperature weather. An individual female usually deposits 100 to 600 eggs. Eggs are greenish yellow and are laid in an ovisac which is about three to four times the body length and entirely covered with white wax. Eggs generally hatch at nearly 10 days and nymph or crawlers pass their times in search of feeding locations. Males have longer developmental time (27-30 days) than females (24-26 days) at (25 ± 1) °C (65 ± 2) % RH and 12:12 (L:D) photoperiod. Indra *et al.,* (2008) observed that female mealybugs usually lay upto 600 eggs enclosed in an ovisac. *P. marginatus* was observed to complete the life cycle on papaya in 26 days and the life cycle was found to vary from 15 days to 32 days depending on the host plant species. It has the ability to develop, survive, and reproduce successfully between 18 to 30 °C which suggests that it has the ability to develop and establish in areas within this temperature range.

The work by Williams and Willink (2003) on effect of temperature on the life history of *P. marginatus* describes that *P. marginatus* capable of developing and completing its life cycle at different temperature regimes. Abiotic factors such as rainfall, temperature and relative humidity, as well as habitat type were found to have an influence on the dynamics and distribution of *P. marginatus* with more effects on crawlers and adults than on egg sacs and on fruits than leaf populations (Cham *et al.,* 2011). The developmental times of *P. marginatus* were found to vary from egg to adult and it was longest at 18 °C for both males and females. Approximately 80-90 % of the eggs survived between 20 and 30 °C. The highest fecundity was at 25 °C with each female producing an average of 300 eggs. Adult longevity, pre-oviposition and oviposition periods increased with decreasing temperature up to 25 $^{0}$C. The proportion of females was 42% at 25 °C and was between 70 and 80 % at 18, 20, and 30 °C. The ability of *P. marginatus* to develop, survive and reproduce successfully between 18 and 30 °C suggests that it has the capability to develop and establish in areas within this temperature range (Amarasekare *et al.,* 2008). A detailed study on effect of thermal stress on biology of PMB was carried out by Amarasekare *et al.,* (2008) at eight different temperatures (15 to 37 °C). At 15, 34, and 35 °C, the eggs hatched after 27.5, 5.9, and 5.5 days of incubation, respectively, but further development of the first-instar nymphs was arrested. The developmental time for egg to adult was the longest at 18 °C for both males and females. Approximately 80 to 90 percent of the eggs survived between 20 and 30 °C. Eggs hatched at all temperatures except 37 °C. Adult longevity, pre-oviposition and oviposition periods increased with decreasing temperature up to 25 °C. Adult male longevity and was the proportion of females was lowest less at 25 °C compared with other temperatures.

Studies on developmental rate of female *P. marginatus* revealed that, the rate of development increased with increase in temperature. During egg stage the developmental rate was four times higher at 32 $^{0}$C than that of 20 $^{0}$C. Developmental rate of all nymphal instars female mealybug showed a negative correlation. Developmental rate of male mealybug was found decreasing with rise in temperature. Studies on effect of thermal stress on developmental biology showed that papaya mealybug eggs failed to hatch at 35 and 40 °C. The time taken by first instar nymph to grow at 20 °C was twice longer than the developmental time at 32 °C. From second instar onwards male and female insects had different developmental duration. In male insect, the developmental time was decreased compared to the preceding stages, whereas it was increased in case of female insects. Developmental period of male insect was longest (13.10 days) at second instar nymphal stages and recorded the minimum at pupal stage (3.5 days). The highest percent survival of eggs recorded at 20 °C. The percent survival of all the nymphal stages shows a fluctuating trend. The survival increased with increasing temperature until 30 °C, above which temperature the survival started to decrease. Pre-oviposition and oviposition periods decreased with increasing temperatures till 30 °C. Pre-oviposition period was longest at lowest temperature (14.8 days) and shortest at 30 °C (4.6 days). Females live longer than male at all temperatures (Laneesha and Shankarganesh, 2016).

Amarasekare *et al.* (2008) showed that *P. marginatus* was able to develop and complete its life cycle at 18, 20, 25, and 30 °C. At 15, 34, and 35 °C, the eggs hatched after 27.5, 5.9, and 5.5 days of incubation, respectively; but, further development of the 1st instar nymphs was arrested. No eggs were hatched at 37 °C.

## Effect of Thermal Stress on Mealybug Parasitoids

*Aenasius bambawalei* Hayat (Encyrtidae: Hymenoptera) is a solitary parasitoid of *P. solenopsis* (Hayat, 2009) parasitised more than 40 percent of the mealybug nymphs (Sharma, 2007). Similarly, about 80 percent parasitization of *P. marginatus* by *Acerophagus papayae* was observed at various places of India. These studies would help in find out the effect of heat stress mediated change on the developmental biology of mealybug pests and their parasitoid fitness, role of stress specific enzyme in thermo tolerance of mealybug pests and their natural enemy will help in formulating effective management strategy of mealybugs and to develop thermal stress tolerant strains of parasitoids. The major natural enemies of *mealybugs* were *A. bambawalei, Cryptolaemus montrouzieri*, *Crysoperla* sp. *Cheilomones sexmaculata, Acerophagus papaya*e, *Spalgis epius* and *Gitonides perspicax* having potential to reduce up to 20-40 % mealybug damage (Nagrare *et al.,* 2011).

Several studies suggest that the host insect and temperature may affect the rate of development and longevity of parasitoids (Deng and Tsai, 1998). Temperature is a key abiotic factor that regulates insect population dynamics, developmental rates, and seasonal occurrence (Campbell *et al.,* 1974; Logan *et al.,* 1976). Temperature-driven rate models are most often used to predict the activity and seasonal population dynamics of pests and natural enemies in field situations. Data on temperature-dependent development of *A. bambawalei* and *A. papayae* reported in the literatures suggested important differences with regard to mealybug species and geographical region. Thus, precise knowledge of the relationship between temperature and rate of development is essential to the formulation of phenological models or studies of population dynamics. Among the biotic factors, the mealybug parasitoids, *A. bambawalei* and *A. papayae*, were found active on mealybug colonies throughout year.

## Stress Enzymes

Exposure of organisms to extreme temperature induces physiological changes in the organisms (Jia *et al.,* 2011). High temperatures significantly increase the oxidative stress and cause over expression of antioxidant enzymes (Davidson and Schiest, 2001a, b). There is constant balance between reactive oxygen species (ROS) and antioxidant enzymes. However, this balance is disrupted during stress conditions and leads to excessive ROS production (Lalouette *et al.,* 2011). Excessive ROS production leads to lipid peroxidation and destabilises cell membrane fluidity, causing apoptosis and DNA damage in the form of degradation, mutations, single-strand scission and base deletions (Green and Reed, 1998; Monaghan *et al.,* 2009). To protect or overcome the damage from ROS, every organism activates an antioxidant defense system during stress condition. This system includes vitamins, antioxidant enzymes, glutathione (Cossu *et al.,* 1997; Wilczek *et al.,* 2004). Superoxide dismutase (SOD), peroxidase (POD) and catalase (CAT) are the key antioxidant defense mechanisms (Felton and Summers, 1995). SOD is considered a very active and strong antioxidant defender that converts its radicals into oxygen and hydrogen peroxide during stress (McCord and Fridovich, 1969), especially when exposed to environmental and thermal stress (Celino *et al.,* 2011; Jia *et al.,* 2011). Catalase also plays active role during the stress condition. It protects organisms by degrading $H_2O_2$ into water and dioxygen before it can harm cellular components (Switala and Loewen, 2002).

Waqas *et al.* (2020) reported that induced heat shock is associated with feeding behaviour, reproduction and reactive oxygen species (ROS) generation that causes oxidative damage and lethal and sublethal effects of heat shock on reproduction, feeding behaviour and antioxidant enzymes, including catalase (CAT), superoxide dismutase (SOD) and peroxidases (POD) in *P. solenopsis* was also studied. Results showed that males were highly susceptible to heat shock treatments than females, as LTemp50 values were 43.8 $^{0}$C for males and 45.11 $^{0}$C for females. Similarly it alter the antioxidant enzymes activities, an increase of CAT, SOD and POD activities were noticed in response to highest intensity of heat shock while a reduction of CAT and SOD activity were noticed in response to lowest intensity of heat shock compared to control (30 °C). These results suggest that heat shock may result in loss of body water and induce oxidative stress in *P. solenopsis*. Temperature induced stress was not only affected the biology and development of mealybugs but also its parasitoids. For instance, increase in temperature negatively affected the performance of *A. papayae* in terms of developmental duration, parasitism efficiency and adult emergence. Exposure of *A. papayae* to different temperatures (25, 28, 30, 32 and 34 °C) led to overall increase in activities of SOD, catalase, POD and glutathione-S-transferases (Shankarganesh *et al.,* 2020).

## Heat Shock Proteins

The heat shock proteins (Hsps) that are abundantly expressed in insects are important modulators of insect survival. Insect heat shock proteins include ATP-independent small heat shock proteins and the larger ATP-dependent proteins, Hsp70, Hsp90, and Hsp60. Synthesis depends on the physiological state of the insect, but the common function of heat shock proteins, often working in networks, is to maintain cell homeostasis through interaction with substrate proteins (Allison *et al.,* 2015). The expression of different Hsp genes are induced and modulated in insects in response to environmental inputs including abiotic stresses such as heat shock, ultraviolet radiation, chemical pesticides, as well as biotic stresses such as viruses, bacteria, fungi and other insects. Fang and Yue (2014) reported that in *P. solenopsis*, experiment on heat shock at 37-45 °C for 1 h and then recovery for 1 h, the relative expression levels of the three Hsp genes increased with the increase of temperature in the three different developmental stages. The correlation analysis suggested that the correlation coefficients between the expression level of the three Hsp genes in all developmental stages and the heat stress temperature were greater than 0:6, except that of *Pshsp*70-4 in female adult (0.225). The expression levels of the three Hsp genes in all tested stages under heat shock at 43 °C and 45 °C for 1 h and then recovery for 1 h were significantly higher than the control group. The expression of heat shock protein genes in *P. solenopsis* is positively correlated with temperature, and PsHsps may play an important role in high temperature tolerance in *P. solenopsis*.

## Models

Crawlers successfully completed development to adult stage between 15 and 35 °C, however, their survival was affected at low temperatures. Thermal constants required for completion of cumulative development of female and male nymphs and for the whole generation were significantly lower on hibiscus (222.2, 237.0, 308.6 degree-days, respectively) compared to cotton. Three nonlinear models performed better in describing the developmental rate for immature instars and cumulative life stages of female and male and for generation based on goodness-of-fit criteria. The simplified β type distribution function estimated Topt values closer to the observed maximum rates. Thermodynamic SSI model indicated no significant differences in the intrinsic optimum temperature estimates for different geographical populations of *P. solenopsis*. The estimated bioclimatic thresholds and the observed survival rates of *P. solenopsis* indicate the species to be high-temperature adaptive, and explained the field abundance of *P. solenopsis* on its host plants (Shreedevi *et al.,* 2013). Fand *et al.* (2014) reported the theoretical lower development threshold temperatures estimated using linear regressions applied to mean development rates were 11.2, 8.9, 9.8 and 12.7 °C, and the thermal constants for development were 93.7, 129.8, 97.1 and 100.0 degree days (DD) for nymph 1, nymph 2, nymph 3 and male pupa stages, respectively. The developed phenology model predicted temperatures between 25 and 35 °C as the favourable range for *P. solenopsis* development, survival and reproduction. *P. solenopsis* population attained a maximum net reproductive rate (107-108 females/ female/ generation) and total fecundity (216.6-226.5 individuals/ female/ generation) at temperatures between 25 and 30 °C. Mean length of generations decreased from 75.6 days at 15 °C to 21 days at 40 °C. The maximum finite rate of increase (1.12-1.16 females/ female/ day) and shortest doubling time (4.3e6.1 days) were also observed at temperatures between 25 and 35 °C. The simulation of phenology model at fluctuating temperatures indicated that *P. solenopsis* populations might potentially increase with a finite rate of 1.06 females/ female/ day with an average generation time of 58.7 days and a doubling time of 12.1 days.

The development duration of female and male nymphal instars linearly decreased with the increase in temperature from 18 to 32 °C. Cumulative developmental time of females ranged from 43.9 d (18 °C) to 15.0 d (32 °C). Survival of crawlers to adulthood was lowest (< 53%) at 20 and 36 °C and highest (80%) at 32 °C. The solenopsis mealybug exhibited obligate sexual ovoviviparous reproduction and the pre-oviposition period in mated females showed a significant decreasing trend between 20 °C (23.0 d) and 30 °C (9.5 d). The oviposition period of 10.2e11.5 d at 25 °C was nearly half the duration than at 20 °C and the highest fecundity (245 eggs þ crawlers) was observed at 30 °C. Longevity of mated females was significantly prolonged at 20 °C (46.0 d) compared to 30 °C (21.4 d). Proportion of females was highest (97.5%) at 25 °C. Males required higher degree-days (363.6) for their cumulative development compared to females (317.5). Lower temperature thresholds estimated from the linear model for cumulative female and male development were 11.7 and 10.1 °C, respectively. The estimated optimum temperature thresholds for nymphal instars (32e33.4 °C) from b type distribution function were closer to the observed maximum developmental rate compared to Lactin-2 model. The population trend index using survival, fecundity, and sex ratio of *P. solenopsis* with an initial population of 100 crawlers in the Morris-Watt life table model indicated a potential population increase of 170.3 and 97.6 times at 30 and 35 °C, respectively, in the next generation.

## Conclusion

Temperature is one of the key factors in distribution and abundance of mealybugs. Global climatic change indirectly influences the existence of sucking pests. These climatic and weather changes not only affect the status of insect pests but also affect their population dynamics, distribution, abundance, intensity and feeding behavior. Not only high temperature thresh hold is responsible for these variation but cool temperature play an important role in intrinsic properties of insect species. This was evidenced by the outbreak different insect pests. Depending on the intensity of change, the climatic ecosystem showed a direct and indirect affect on the mealybugs and their natural enemies. The optimum temperature for growth and development mealybugs were very well explained by several authors. Depending on the stage of exposure of the insect to extreme temperature, influences the mealybug to create havoc in the agro-ecosystem.

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