



DIAPAUSE IN *CHILO PARTELLUS*: A RESEARCH JOURNEY

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ABSTRACT

Spotted stem borer, *Chilo partellus* (Swinhoe) is one of the most widely distributed pests of coarse cereals, causing 18 to 25% yield losses in Asia and Africa. The larvae of *C. partellus* pass through hibernation under North Indian and aestivation under South Indian conditions. Although diapause helps *C. partellus* in adapting under unfavorable conditions, there is 17.2 to 28.3% and 7.0 to 33.7% population sacrifice during hibernation and aestivation, respectively. The population heterogeneity in *C. partellus* could be due to hibernation or aestivation, wherein the models, Ikemoto & Takai (linear), and Lactin-1 and Lactin-2 (non-linear) are efficient for describing temperature-dependent development and estimating the temperature thresholds of diapausing larvae. This helps in predicting the occurrence, seasonal emergence, number of generations and population dynamics of the pest. Diapause results in differential regulation of hormonal and biochemical profiles, impose deleterious effects on the post-diapause development, reproductive physiology and population growth of *C. partellus*. The diapause, developmental and morphometric traits in *C. partellus* are governed by overdominance gene effects which mainly depend on parental diapause history. Four different biotypes of *C. partellus* viz., Hisar, Hyderabad, Parbhani and Coimbatore exist in India, suggesting that sorghum and maize genotypes need to be tested against these four populations to identify stable sources of resistance. The whole genome sequencing will be useful for understanding mode of action of different insecticides, mechanisms of detoxification and designing target-specific insecticides to develop appropriate strategies to manage *C. partellus* for sustainable crop production. The temporal distribution of mating systems among adults of diapause, non-diapause and/or ecologically diverse populations, and their behavioral and physiological consequences under a given demographic framework could be rewarding, and aid in to devising appropriate mating disruption techniques to suppress *C. partellus* population.

Key words: Spotted stem borer, *Chilo partellus*, diapause, hibernation, aestivation, genetics, biotypes, hormonal regulation, biochemical profile, reproductive physiology

The term diapause was used first time for the eggs of grasshopper, *Conocephalus ensiferum* (Wheeler, 1893). In general, diapause is retardation in normal growth and development process under unfavourable environmental conditions, and is often confused with quiescence. The diapause has been defined differently by earlier workers: Andrewartha (1952) "A stage in the development of certain animals, during which morphological growth and development are suspended or greatly decelerated"; Beck (1962) "State of arrested development in which the arrest is enforced by a physiological mechanism rather than by concurrently unfavourable environmental conditions"; and Tauber et al. (1986) "Diapause is a neuro-hormonally mediated, dynamic state of low activity that occurs during genetically determined stage(s) of metamorphosis, usually in response to environmental stimuli that

precede unfavourable conditions". Diapause is classified according to the season (winter diapause - hibernation and summer diapause - aestivation), stage of life cycle (egg/embryo, larval, pupal and adult/reproductive diapause), facultative and obligatory (governed by environmental variations and genetic factors, respectively), and intensity (intense and shallow diapause).

Diapause has evolved as an important life history component, and is a genetically programmed physiological state of arrested metabolic activity that occur at a specific stage under predictable unfavorable environmental factors. During diapause insect passes through a series of hormonally mediated physiological events like induction, maintenance, termination and post-diapause development. The insects are encountered with several physiological (suppression

of metabolic activity), morphological (weight, size, body colour, pigmentation and sclerotization), and behavioural (cessation of feeding, exceeding normal developmental time and construction of resting sites) changes during the diapause. Several hormones are responsible for sequential changes during the developmental process in insects from one stage to another, like prothoracicotrophic hormone, ecdysone (α -ecdysone and 20-hydroxyecdysone or β -ecdysone), juvenile hormone, etc. The fluctuation in the levels of ecdysteroids and juvenile hormone titres also takes place during different stages of diapause.

Past few decades, the ecological and physiological significance of the deteriorating effect on post-diapause development in terms of costing directly to population growth and indirectly on changes in the pattern of allocation of available metabolic reserves have attracted attention as having implications for post-diapause longevity, reproductive investments, performance and fecundity (Tauber et al., 1986). Plant biochemistry is also differentially expressed under different climatic conditions, thus altering the nutritional quality of the host plant which affect the differential insect-plant interaction under given agro-ecological conditions. Genetic determination of locally adapted life-history traits like diapause and polyphenism are also important to understand bio-ecology and population dynamics of insects in response to abiotic and biotic factors. The cross-mating among the adults of diapause and nondiapause strains across geographical regions is very likely, and there is a possibility of genetic polymorphism within and/or among the insect populations leading to evolution of different biotypes/ecotypes. Unfortunately, no phenological model is available to predict seasonal emergence from diapause experiencing insect populations and population regulation mechanism.

Spotted stem borer, *Chilo partellus* (Crambidae: Lepidoptera) first described by Swinhoe in 1885, is one of the most widely distributed species of *Chilo* in the tropics. *Chilo partellus* is native of Asia, but in the 1950s it got established in East Africa, and

since then has spread to southern and central Africa. Recently, it posed a serious risk of invasion in the Americas, Australia, China, Europe, New Zealand and West Africa due to congenial environment, host crops and agronomic practices (Yonow et al., 2017). It is an established pest of maize, sorghum, sugarcane and rice, and has also been recorded from small millets and wild grasses, causing 18 to 25% yield losses in maize and sorghum in Asia and Africa (Dhaliwal et al., 2015). The presence, abundance and intensity of infestation by *C. partellus* is influenced by both biotic and abiotic factors, wherein the morphological, behavioural, physiological and bioecological variation makes it to survive under diverse and adverse agroecological conditions. *Chilo partellus* undergoes facultative diapause as mature larvae inside the old stems or stubbles of host plants (Kfir, 1991; Ofomata et al., 1999). Moreover, the larvae of *C. partellus* pass through hibernation under North Indian and aestivation under South Indian environmental conditions. There had been limited success in deciphering underlying mechanisms and finding novel solutions for the management of *C. partellus* due to non-availability of genomic resources. The whole genome sequencing can also help in understanding the role of specific genes involved in production of heat- or cold-shock proteins to adapt to diverse and adverse environmental conditions. This manuscript aims at giving the overview of the studies carried out on various aspects of diapause in *C. partellus*.

TYPES OF DIAPAUSE IN *CHILO PARTELLUS*

Hibernation

Determination of critical threshold for induction and termination of hibernation are important for better understanding the bio-ecology and population dynamics of *C. partellus* under varying climatic conditions. The induction of hibernation in *C. partellus* larvae takes from 46 to 56 days depending upon temperature and photoperiod conditions (Dhillon et al., 2017). Induction of hibernation varied from 7.9 to 18.3%, $22 \pm 1^\circ\text{C} + 11.5\text{L}:12.5\text{D}$ being the optimum

under laboratory conditions, showing that not all *C. partellus* larvae undergo hibernation under prevailing environmental conditions. The larvae of *C. partellus* undergoing hibernation experienced significant reduction in weight, length and head capsule width. Termination of hibernation occurred between 8 to 12 days on exposure to ambient conditions, underwent up to five supernumerary moults, and their developmental time varied from 94.9 to 160.4 days (Dhillon et al., 2017). Due to hibernation, a population loss of 17.2 to 28.3% was recorded in *C. partellus*, which has implications for population build-up of post-hibernation first brood and management strategies (Dhillon et al., 2017).

Aestivation

Diapause is an important adaptive trait and correct combination of temperature, photoperiod and food quality are important for aestivation in *C. partellus*. The process of aestivation initiation was faster at 35°C+ 13.5L:10.5D, but highest number of larvae (61.7 to 65%) entered aestivation between the 30°C+12.5L:11.5D to 32°C+13L:11D temperature and photoperiod conditions in the laboratory (Dhillon et al., 2019a). The exposure to 30°C+12.5L:11.5D and 32°C+13L:11D along with dry food initiated the process of aestivation and were found optimum for induction of aestivation in *C. partellus*. There was significant increase in weight, length and head capsule width of *C. partellus* larvae with increase in temperature and photoperiod treatments up to a certain age and duration of exposure during the process of aestivation. As per Dyar's ratio overall head capsule width progressed geometrically with minimum constant ratio of 1.20, and second-degree polynomial regression equations were best fitted (Dhillon et al., 2019a). During the aestivation process, there was 7.0 to 33.7% larval mortality in *C. partellus* under varying temperature and photoperiod conditions, indicating that the immature stages in *C. partellus* have high sensitivity to changing climatic conditions (Dhillon et al., 2019a).

TEMPERATURE-DEPENDENT DEVELOPMENT

The temperature-dependent development rate models are important for predicting the occurrence, seasonal emergence, number of generations and population dynamics of *C. partellus*, which could also be highly useful to predict seasonal emergence of *C. partellus* from diapause experiencing populations. Temperature-dependent development rate of diapausing larvae of *C. partellus* examined on 13 constant temperatures ranging from 8 to 40°C found that the development of hibernating and aestivating larvae occurred from 10 to 25°C and 27 to 38°C, respectively, and no development occurred at 8°C and 40°C (Dhillon and Hasan, 2017a). The diapausing larvae require a thermal constant between 333 – 338 degree-days to complete their development right from initiation to termination of diapause. The physiological response to below optimum fluctuation in temperature and photoperiod conditions disrupt growth and development in *C. partellus*, thus accumulating more numbers of degree-days (Khadioli et al., 2014). We established that the Ikemoto and Takai linear model and Lactin-2 followed by Lactin-1 non-linear models are useful and efficient for describing temperature-dependent development and estimating the temperature thresholds of diapausing larvae of *C. partellus* (Dhillon and Hasan, 2017a). However, the degree-days accumulation in post-diapause development is essential for accurate prediction of insect population appearance and better understanding on the phenology of *C. partellus*.

MORPHOLOGICAL CHANGES

Diapause state is very rarely accompanied by morphological characteristics that permit their easy identification. A detailed diagnostic key based on photographs was established to differentiate diapausing and nondiapausing larvae of *C. partellus* (Dhillon and Hasan, 2017b). There is polymorphism in mature nondiapausing and diapausing (aestivation/hibernation) *C. partellus* larvae, and during diapause it moults several times designated as supernumerary moults. The mature spotted *C. partellus* larvae when

exposed to diapause inducing conditions (aestivation/ hibernation), are first transformed into diapause and nondiapause transitional morphs, wherein the cervical shield and pinaculae are less pigmented than in spotted morphs (Dhillon and Hasan, 2017b). The transitional *C. partellus* morphs within one to two days are transformed into immaculate larvae, which are without pigmentation around the setae having uniform milky white colour, and indicate the onset of diapause. The size of diapause larvae is much reduced, the cuticular pigmentation disappear and body colour turns creamy to milky white, while nondiapause larvae remain light brown with dark brown to black spots (Dhillon and Hasan, 2017b). The aetose tubercles disappear in diapause larvae, the head capsule colour in diapause larvae turns reddish brown with blur epicranial suture, being dark brown to black with distinct epicranial suture in nondiapausing larvae. The colour of prothoracic shield turns light brown to creamish in diapausing larvae, while dark brown in nondiapause larvae. The diapause larvae fail to pupate, construct a diapause chamber and exceed normal development time by exhibiting at least >2 supernumerary moults. Kfir (1991) also reported seven supernumerary moults in diapausing *C. partellus* larvae. The size of pupae from the diapause experiencing larvae was reduced, and adults emerged were also comparatively smaller in size and darker in colour than those from nondiapause larvae (Dhillon and Hasan, 2017b).

PHYSIOLOGICAL CHANGES

The regulation of aestivation and hibernation diapauses i.e., induction, maintenance and termination and the responsible factors are very much known in *C. partellus* (Scheltes, 1978; Dhillon et al., 2017, 2019a). Diapause is not always an adaptive advantage to insects, if it enters diapause early in the season or delay in emergence from diapause lead to copulation disruption and laying of unfertilized eggs, while delayed entrance or early termination of diapause might expose to harsh climatic conditions (Arbab, 2014). It was not clear whether the diapause in *C. partellus* cause any deteriorating effect on post-diapause development

and subsequent life history traits like survival rate of adults, fecundity, progeny viability and other population growth factors undergoing diapause. Such effects have ecological and physiological significance in terms of costing directly to population growth and/or indirectly on diapause strategy of individuals, as a result of changes in the pattern of allocation of metabolic reserves. The larval diapause in *C. partellus* has considerable effect on various important post-diapause biological traits such as time taken and success in pupation, adult emergence, reproductive performance and reproductive investments by the adults, and several other population growth parameters (Dhillon and Hasan, 2018). The percentage pupation was considerably low in hibernating followed by aestivating and nondiapausing *C. partellus* larvae. This low rate of pupation in diapause experiencing *C. partellus* populations can be explained in terms of losses (hibernation: 17.2–28.3%; aestivation: 14.0–40.0%) due to different kinds of diapause (Dhillon et al., 2017, Dhillon and Hassan, 2018). The weights of male and female pupae obtained from diapause experiencing *C. partellus* larvae were lighter could be due to lighter weights of diapausing larvae. Adult emergence, sex ratio, and body weight and longevity of *C. partellus* adults were also found negatively affected by diapause. Tamiru et al. (2012) also reported that the cooling and freezing, and rates of temperature change influences the physiology of *C. partellus*, thus leading to effects on morphological traits like larval weight, length and head capsule width. The females emerging from nondiapausing population were heavier in weight and their ovaries contained more egg cells than the females obtained from diapause experienced population. The numbers of egg cells in ovaries of *C. partellus* females were positively correlated with their body weight, and the reduction in post-diapause female reproduction could be attributed to decrease in their body weight and longevity. Mating success of *C. partellus* males from aestivation and hibernation experiencing populations was significantly lower than those from non-diapausing ones, which could be due to compromised physical condition and/

or physiological response of such males in terms of pheromone response while attempting courtship with counterpart females (Dhillon and Hasan, 2018). Moreover, we have also found significant difference in spermatophores in bursa copulatrix of females from diapausing and non-diapausing populations. Similarly, the quantity of eupyrene sperm transferred by the males also differed significantly between the individuals obtained from non-diapause and diapause populations. The *C. partellus* females from diapausing population had shorter oviposition period, lower fecundity, and higher percentage of sterile eggs, indicating the poor reproductive performance of females and qualitative/quantitative decrease in male ejaculates. The larval diapause in *C. partellus* decreases female fecundity leading to reduction in net reproductive, intrinsic and finite rates of increase, thus resulting in an increase in mean generation and development time. It is now clear that the diapause incurs the poor reproductive performance of female and male adults in terms of reduced fecundity, egg viability, deposition of spermatophores in bursa copulatrix and numbers of eupyrene sperms, thus have a physiological cost to diapausing *C. partellus*.

BIOCHEMICAL CHANGES

Proteins, lipids and carbohydrates are major sources of energy for the insects, which also help in maintaining the suppressed metabolism during diapause and post-diapause development. A wide array of small molecules like amino acids, lipids, polyols, fatty acids and metabolic intermediates could also be helpful in metabolic adjustments during diapause in the insects. Total protein content was found greater during diapause in aestivation than in hibernation *C. partellus* larvae could be because of synthesis of additional heat shock proteins to sustain during aestivation (Tanwar, 2022). The higher total protein content in pupae than the larvae from all the diapause and nondiapause strains of *C. partellus*, suggest their greater requirement during pupation to support the development of different adult features and organs. The amino acids like serine, glycine, histidine, arginine, proline, tyrosine and

methionine were in higher titres in aestivation than hibernation and nondiapause larvae which could be imparting heat-shock tolerance during aestivation (Tanwar et al., 2021). The hibernation larvae hoarded low amounts of amino acids as compared to aestivation larvae which might be helpful in maintaining metabolic homeostasis as a result of cold stress. Further, the similar amounts of aspartic acid, glutamic acid and alanine in hibernation and nondiapause, and that of threonine, valine, isoleucine, phenylalanine and leucine in aestivation and nondiapause *C. partellus* larvae suggest that these amino acids could be specifically required for maintaining the hibernation and aestivation, and post-diapause biological and physiological functions (Tanwar et al., 2021). As cystine has been found to contribute in plant defense against *C. partellus* (Dhillon and Kumar, 2017), and absence in diapause and presence in the nondiapause larvae suggest that this amino acid is not essential during the non-feeding stage, i.e., diapause. The higher amounts of test amino acids in aestivation than hibernation larvae of *C. partellus* could be to meet the greater energy requirement while dealing with heat-shock proteins during aestivation (Tanwar et al., 2021). Total lipid content was found higher in the nondiapause larvae and pupae in comparison to hibernation and aestivation strains of *C. partellus*, suggesting that the stored lipids are being utilized to maintain the diapause development, which are also left with small amounts to be transferred in the pupae (Tanwar, 2022). The higher total lipid content in the larvae from hibernation than the aestivation strain suggest that higher amount of lipids is required to support the hibernation, as is not the case with aestivation strain of *C. partellus*. The higher amount of lipids in the hibernation and nondiapause larvae than pupae, and higher amounts in pupae than larvae of aestivation strain suggest that the aestivation larvae might be requiring more proteins than lipids to sustain the diapause, and the lipids are transferred to the pupae to support the development of different adult features and organs. The total lipid content was significantly higher in the *C. partellus* larvae at initiation and during hibernation as compared

to aestivation, which could be to conserve the energy to support during the hibernation (Tanwar, 2022). The lower linoleic acid, stearic acid, eicosanoic acid and n-pentadecanol contents in hibernation than aestivation and nondiapause larvae of *C. partellus* suggest that these lipophilic compounds could be required for various metabolic and physiological activities (Tanwar et al., 2021). The higher palmitoleic acid and methyl 3-methoxytetradecanoate contents in hibernation, and higher myristic acid and lathosterol contents in aestivation larvae suggest that these lipophilic compounds impart cold-shock and heat-shock tolerance, respectively. The higher cholesterol, and lower squalene and gamma-ergosterol contents in hibernation and aestivation than nondiapause larvae indicate their important role in maintenance of diapause in *C. partellus*. The higher palmitoleic acid and methyl 3-methoxytetradecanoate contents in hibernation, and higher myristic acid and lathosterol contents in aestivation larvae suggest that these lipophilic compounds impart cold-shock and heat-shock tolerance, respectively. However, the exact role of the test amino acids and lipophilic compounds in various processes like induction, maintenance and termination of hibernation and aestivation in *C. partellus* need to be explored through more advanced biochemical pathway analysis to establish better understanding on their function in diapause.

HORMONAL REGULATION

Several hormones are responsible for sequential changes during the developmental process in insects from one stage to another, like prothoracicotropic hormone, ecdysone (α -ecdysone and 20-hydroxyecdysone or β -ecdysone), juvenile hormone, etc. Fluctuation in the levels of ecdysteroids and juvenile hormone titres have been observed during different stages of diapause in several insects. There were varying levels of α -ecdysone, β -ecdysone or 20-hydroxyecdysone and juvenile hormone at different stages of diapause in the larvae and pupae from hibernation, aestivation and nondiapause strains of *C. partellus* (Tanwar, 2022). The α -ecdysone titre was

significantly greater in the hibernation both at initiation and during diapause as compared to aestivation in *C. partellus*. At the initiation of both hibernation and aestivation, the 20-hydroxyecdysone titre was greater than α -ecdysone, while during diapause it decreased in hibernation but increased in aestivation over that of α -ecdysone in the larvae of *C. partellus* (Tanwar, 2022). Across the *C. partellus* diapause strains, the α -ecdysone titre was higher during the diapause than at the diapause initiation stage. The α -ecdysone was significantly higher in the larvae from hibernation, while it was significantly greater in the pupae from aestivation as compared to respective diapause and nondiapause strains of *C. partellus*. However, the 20-hydroxyecdysone in the larvae and pupae from aestivation was significantly greater than those from hibernation and nondiapause *C. partellus*. The 20-hydroxyecdysone level increased over the α -ecdysone in the pupae from hibernation, while reverse was the case for aestivation and nondiapause *C. partellus* (Tanwar, 2022). These findings suggest that the type of diapause and/or nondiapause regulates the ecdysteroid levels (α -ecdysone and 20-hydroxyecdysone) depending on the developmental stage and state of *C. partellus*, which could be essential to trigger and maintain the diapause, resume post-diapause growth and development, and pupal/adult apolysis (Tanwar, 2022). The juvenile hormone titre was higher at the diapause initiation than during the diapause, which was again greater in the pupae than the larvae across diapause and nondiapause strains of *C. partellus*. The juvenile hormone titre was significantly greater in the aestivation both at the diapause initiation and during diapause as compared to hibernation strain of *C. partellus*. The juvenile hormone titre was significantly greater in the pupae from nondiapause than those from diapause strains and was on par in the hibernation and aestivation strains of *C. partellus*.

GENETICS OF DIAPAUSE

Both temperature and photoperiod combine are critical for induction and termination of diapause in *C. partellus* (Dhillon et al., 2017; 2019a). Varying

photoperiod and temperature regimes, and different cross-mating combinations are integral to better understand the inheritance of diapause in insects. It is very likely that the adults of diapause and nondiapause strains and their F_1 progenies within and across geographical regions cross-mate resulting in genetic polymorphism in *C. partellus*. To gain an understanding of importance of diapause for ecological adaptation, it is important to study regulation of diapause. We used all the strains of *C. partellus* like hibernation, aestivation, nondiapause, their progenies in all possible combinations including reciprocal crosses, and observations were recorded on fecundity, egg hatching, larval survival, diapause induction and termination, adult emergence, and morphometrics of larvae, pupae and adults in the parents (P_1 , P_2), F_1 hybrids, and the reciprocal crosses (Dhillon et al., 2020). Genetic analysis showed that aestivation strain is a general combiner, which also improved egg hatching, larval survival, diapause termination, adult emergence and proportion of females in the progenies. Incidence of diapause was highest in hibernation \times aestivation, whereas termination was greatest in post-hibernation (F_1 progenies of hibernation) \times aestivation. However, nondiapause strain and its reciprocal crosses with other strains did not exhibit any noticeable developmental response associated with diapause. Specific combining ability analysis suggested that where post-hibernation and aestivation strains exist together there will be likely reduction in diapause incidence, increased survival with greater fitness and faster multiplication of their progenies resulting in outbreak of *C. partellus*. The degree of dominance estimates for diapause, developmental and morphometric traits revealed that these traits are governed by overdominance gene effects, and mainly depend on parental diapause history in *C. partellus* (Dhillon et al., 2020). The diapause incidence could be prerequisite for rapid adaptation to prevailing environmental conditions, and have implications for exploring appropriate genetic means of *C. partellus* management under different agro-ecological conditions.

CONSEQUENCES ON MATING SYSTEM

The emergence of *C. partellus* adults after diapause could result in mating asynchrony, thus leading to deleterious effects on reproductive physiology and progeny production. We investigated effects of mating among different aged males and females (1, 2 and 3-day old) in all possible combinations on reproductive physiology, progeny production and longevity of *C. partellus* adults. The fecundity, fertility, hatchability, and longevity of male and female adults were recorded. The mating among old aged males and females significantly reduced the fecundity, fertility and egg hatchability (Dhillon et al., 2019b). The fecundity, fertility and egg hatching were significantly higher when newly emerged females mated with males of either ages as compared to other mating treatments. Conversely, the three-day old females when mated with males of either of the ages laid more numbers of unfertilized eggs, thus reduction in egg hatchability. Mating among newly emerged adults significantly reduced the longevity of male and female adults. Kaplan-Meier estimation showed that none of the adults across mating treatments survived more than six days. The recovery of spermatophores from the reproductive tract of females from 3DM \times 1DF was significantly higher than other mating treatments. However, no association was found between spermatophore recovery and longevity of male and female adults (Dhillon et al., 2019b). These findings could be helpful in devising appropriate techniques to disrupt mating and suppress *C. partellus* population.

INSECT-PLANT INTERACTION

There is significant phenotypic variation in adults of *C. partellus* under diverse ecological regions of India (Dhillon et al., 2022b). The biological performance and biochemistry of the insect from different ecological conditions vary while feeding on diverse host plant genotypes, and plant biochemistry is also differentially expressed under different climatic conditions, thus leading to variable herbivore-plant associations (Dhillon et al., 2021; Samal et al., 2022). There is variation in damage potential, biological attributes and

biochemical profiles of *C. partellus* populations from different geographical regions infesting sorghum and maize in India (Dhillon et al., 2021). The similarity index based on virulence, biological attributes, and amino acids and lipophilic profiles placed the *C. partellus* populations in six groups. The *C. partellus* populations from Hisar, Hyderabad, Parbhani and Coimbatore were distinct from each other, suggesting that there are four biotypes of *C. partellus* in India (Dhillon et al., 2021). As the type and intensity of diapause exercises a profound effect on post-diapause development and reproduction (Dhillon and Hasan 2018), it is possible that progenies from aestivation, hibernation and nondiapause *C. partellus* display differential host preference, damage and larval survival on the known resistant and susceptible host crop genotypes. The larval weight and survival, leaf damage and deadhearts by hibernation, aestivation and nondiapause strains of *C. partellus* were significantly higher in the susceptible than in the resistant maize genotype. However, the larval weight and survival, leaf damage and deadhearts were significantly greater by the larvae from hibernation strain in the susceptible maize genotype as compared to those from aestivation and nondiapause *C. partellus* strains (Tanwar, 2022). Thus, sorghum and maize genotypes need to be tested against these four populations to identify stable sources of resistance. Future studies on gene flow across geographical regions through molecular approaches could also be helpful in establishing the distinctness of different biotypes of *C. partellus* in India.

MOLECULAR INSIGHTS

The biological experiments are good at understanding various dimensions of insect life, however underlying mechanisms, their functions and the genes responsible can only be best understood by getting their genomic fingerprints. The whole genome sequencing could be helpful in understanding the phylogeny, endocrine system, metabolism, diapause physiology, biological processes, mechanisms of insecticide detoxification, insecticide resistance, discovery and synthesis of target site-specific insecticide molecules, and role of specific

genes involved in production of heat- or cold-shock proteins to adapt to diverse and adverse environmental conditions. The whole genome of *C. partellus* from three diverse sources was sequenced using the Illumina HiSeq 2500 platform, which resulted in identification of 64 Cytochrome P450 genes, and 36 glutathione S-transferases genes encoding metabolic detoxification enzymes, primarily responsible for xenobiotic metabolism in insects (Dhillon et al., 2022a). In addition, target receptors related to insecticide action, 4 acetylcholinesterase, 14 γ -aminobutyric acid, and 15 nicotinic acetylcholine receptors were also detected (Dhillon et al., 2022a). These findings will be useful for understanding mode of action of different insecticides, mechanisms of detoxification and designing target-specific insecticides to develop appropriate strategies to control *C. partellus* for sustainable crop production.

CONCLUSIONS

Diapause is although an adaptive mechanism to survive unfavorable conditions, there is considerable population sacrifice during hibernation (17.2 to 28.3%) and aestivation (7.0 to 33.7%). Not all larvae undergo hibernation or aestivation and could be responsible for population heterogeneity in *Chilo partellus*. The Ikemoto & Takai (linear), and Lactin-1 and Lactin-2 (non-linear) models are efficient for describing temperature-dependent development and estimating the temperature thresholds of diapausing larvae of *C. partellus*, which could be useful for predicting the occurrence, seasonal emergence, number of generations and population dynamics of *C. partellus*. Diapause has been found to have deleterious effects on the post-diapause development, reproductive physiology and population growth in *C. partellus*. The biochemical profiles are differently regulated during diapause, some of them could be constituents of heat-shock proteins and help in maintaining development during hibernation and aestivation in *C. partellus*. Degree of dominance estimates revealed that diapause, developmental and morphometric traits in *C. partellus* are governed by overdominance gene effects, mainly depend on parental diapause history,

and suggest to explore appropriate genetic means of *C. partellus* management under different agro-ecological conditions. Four different biotypes of *C. partellus* viz., Hisar, Hyderabad, Parbhani and Coimbatore exist in India, suggesting that sorghum and maize genotypes need to be tested against these four populations to identify stable sources of resistance. The temporal distribution of mating systems among adults of diapause, nondiapause and/or ecologically diverse populations, and their behavioral and physiological consequences under a given demographic framework could be rewarding, thus suggest to devise appropriate mating disruption techniques to suppress *C. partellus* population under field conditions. The whole genome sequencing will be useful for understanding mode of action of different insecticides, mechanisms of detoxification and designing target-specific insecticides to develop appropriate strategies to control *C. partellus* for sustainable crop production.

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