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Sub-lethal effects of indigenous isolate of *Spodoptera frugiperda* nucleopolyhedrovirus on fall armyworm growth and reproduction in India

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Abstract

Background Baculoviruses are specific pathogens which can lethally infect several lepidopteran pests. However, the sub-lethal effects of baculoviruses are also highly debilitating for the host. The objective of the study was to demonstrate the sub-lethal effects of an indigenous strain of *Spodoptera frugiperda* nucleopolyhedrovirus (SpfrNPV) infecting fall armyworm in India.

Results As a result of larval infection, the larval developmental time was significantly prolonged as compared to the untreated insects. The percentage of pupal mortality ranged from 40.74 to 72.73 at varying doses of SpfrNPV and recorded low pupal weight in all the treatments than control. The fertility and fecundity of infected adult moths was significantly reduced when compared to the untreated insects in a concentration dependent fashion. Sub-lethal effects of baculoviral infection on different biological parameters were studied. Mean developmental period of infected 3rd and 4th larval instars was significantly higher ($F = 2.945$; $F = 18.414$; $df = 5, 20$; $P < 0.05$) in SpfrNPV infected larvae than the control at all tested viral concentrations. The percentage of pupal mortality ranged from 40.74 to 72.73 in the lowest and highest concentrations of SpfrNPV, respectively. Developmental period of male pupae was found to be significantly longer in infected groups than the uninfected ones. The infected adults had significantly reduced longevity in both males ranged from 3.5 to 5.75 ($F = 6.273$; $P = 0.002$) and females ranged from 3.5 to7.00 ($F = 13.652$; $P = 0.001$). Further, the mates of virus-treated adults showed a highly reduced egg production ($F = 31.255$; $P < 0.05$) ranged from 150.03 to 338.33 and the larval emerging ranged from 71.11 to 227.89 ($F = 74.52$; $P < 0.05$), which was again significantly lower than the control. The percentage of egg hatching ranged from 47.40 to 86.41%.

Conclusions The sub-lethal effect of SpfrNPV has observed on the growth and development and also reduced percentage of egg hatching in the subsequent generation. Hence, this indigenous SpfrNPV strain can be used in the sustainable and resilience IPM program. Further studies under open field conditions are still needed.

Keywords Sub-lethal effect, *Spodoptera frugiperda*, Nucleopolyhedrovirus, Growth reproduction

Background

In late 2016, fall armyworm (FAW) *Spodoptera frugiperda* (J.E. Smith) (Lepidoptera: Noctuidae) was first reported outside America from West Africa and within three years it had spread to more than 40 countries in Africa (Sisay et al. 2019). Thereafter, it has spread to

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different countries in South Asia including India (2018) and was recently reported from Australia (CABI 2020). In Asia, FAW was first detected and confirmed in Indian state of Karnataka (Shylesha et al. 2018). Within less than five months of first appearance, it was confirmed in five other states: Tamil Nadu, Telangana, Andhra Pradesh, Maharashtra and West Bengal in maize as well as sugarcane crops (Bhosale 2018). Maize is considered to be the most important crop in India after rice. In India, the damage was observed on leaf, silk and tassel with damage levels ranging between 25 and 55.9% and subsequent loss of grain yield by 11.57–58% (Chimweta et al. 2020).

Inherent entomopathogens of related existing pest species is the main defense step against invasive pest management. Native entomopathogens found to infect FAW in India were *Metarhizium rileyi*, *Beauveria bassiana,* nucleopolyhedrovirus and *Bacillus thuringiensis* (Sivakumar et al. 2020). Among the entomopathogens, SpfrNPV is highly species-specific and causes the natural mortality of 21.57–23.28% in south India (Sivakumar et al. 2020). Baculoviruses are considered as propitious viral bio-control agents and are recognized as eco-friendly, non-toxic, and safe to non-target organisms unlike conventional chemical pesticides. They can persist outside the host for considerable periods as occlusion bodies (OBs), which can initiate infection after they are ingested by the susceptible hosts (Gramkow et al. 2010). Larvae infected with lethal concentrations of baculoviruses are usually less active and have slow growth and development, hence giving way for easier parasitization and predation by natural enemies. This interaction of natural enemies provides more possibility for their multiplication, therefore leading to the suppression of pest population in the field conditions (Fan et al. 2008). Thus, the use of baculoviruses in bio-control of agriculturally important insect pests is gaining importance in the environment as limited biocontrol pathogens (Kroemer et al. 2015). The enhancement of occlusion body formation and their mode of action is determined by the potentiality of the viral biopesticide and in the development of their highly virulent strain (El-Menofy et al. 2014).

However, while searching for virulent native baculoviral strains, emphasis is generally placed on the isolates causing higher lethality. The sub-lethal effects of baculoviruses are often not taken into account while checking the efficacy of a novel strain. It is well known that baculoviral infection has a great impact on insect development and its growth in the surviving population and hence leading to reduction in its fertility and fecundity (Myers et al. 2000). Low virulent strains of baculovirus are also known to possess the ability to transmit themselves vertically to the next generation (Williams et al. 2017). The spontaneous outbreak of baculovirus epizootics in healthy insects was seen due to the covert infection of the virus (Myers and Cory 2016).

In the present study, the effect of indigenous strain of SpfrNPV on the larval growth, pupal development and the reproductive potential of the surviving FAW adults at different doses of SpfrNPV infection were evaluated. Potential of SpfrNPV strain to be vertically transmitted to the next generation at varying doses of infection was also investigated. The novel strain of baculovirus should be tested on both their lethal and sub-lethal effects on the target population to understand the gross effect of the virus on pest control.

Methods

Target pest

The target pest species used in this study was obtained from ICAR-National Bureau of Insect Resources (NBAIR), Bengaluru. Fresh castor leaves were used to rear the early instars' larvae in insect plastic breeding containers ($30 \times 15 \times 6$ cm), and maize leaf powder based artificial diet (Wang et al. 2019) was provided for 3rd instar larvae until pupation by maintaining the laboratory conditions at 26 ± 2 °C and 70 ± 5% relative humidity (RH). After emergence of adult moths from the collected pupae, a white paper was wrapped inside the plastic container (45×20 cm) for oviposition along with which 10% honey solution was also provided for their survival. Further the eggs laid were separated and kept for larval emergence under laboratory conditions. Five-day old larvae and/or approximately 2nd instar larvae were used in this study.

Isolation and mass production of virus

Collection of infected *S. frugiperda* larvae was carried out during epizootic in September 2020 at a field near to Chikkabalapur, Bangalore India. The infection was confirmed through one of its characteristic symptom like the dead larvae hanging on the top of the whorl of maize plant. The field collected infected larvae was further processed for purification at ICAR-NBAIR Bangalore. The process of purification was done by first homogenizing the diseased larvae with sterile distilled water, which was later filtered twice by using a muslin cloth where the larval debris was removed. Homogenized filtrate was spun at 1000 rpm for 1 min and 8000 rpm for 15 min continuously where a purified pellet was obtained and it was dissolved in water. Pure OBs were counted by using Neubauer hemocytometer and their morphology was observed under 400X magnification light microscope. The molecular confirmation of SpfrNPV was done by obtaining amplification of polh gene by using specific SpfrNPV primers and the confirmed nucleotide sequence was submitted to NCBI GenBank for which the accession

number (MT422725) was received (Sivakumar et al. 2020). This viral inoculum was used at the entire study.

Diet surface contamination bioassay

In this experiment, late 2nd instar larvae were used. Experimental larvae were maintained separately by the individual egg masses after they hatch and the neonate larvae were provided with tender caster leaves. Larvae of 6th day old and /or approximately 2nd instar larvae were used. Individual 5 ml plastic vials were selected and added approximately 1 ml of artificial diet. Five different concentrations of SpfrNPV OBs: 1.18×10^7; 2.8×10^6; 2.0×10^6 1.2×10^5 and 3×10^4 OBs per 100 µl and one control (sterile distilled water) were used. Inoculation of 100 µl OBs suspension on the artificial diet was undertaken to each larval replicate uniformly. Individual larvae were observed for the period of their larval duration and their developmental time until the adult emergence. Larvae were individually allowed to feed on these treated diets and only those larvae, which entirely consumed the treated diet within 3 days, were included in the test and transferred to 500 µl of fresh diet and reared up to pupation stage. Each treatment was replicated five times with 20 plastic vials/replicate (100 plastic vials/treatment). Deaths due to polyhedrosis infection were recorded at larval and pupal stages and the dead larvae/pupae were monitored for presence of occlusion bodies. Survived individuals were subjected to examine the sub-lethal effect of baculovirus infection on different biological parameters.

Adult developmental period and reproductive ability

The survived pupae were separated (5 pupae/replication) individually, and individual pupae were weighed and their respective sexes were distinguished. Some pupae showed a characteristic of oozing of haemolymph from the pupae and some adults showed a typical symptom of wing deformation (Fig. 1). Virgin and freshly emerged healthy adults (< 48 h old; 2 pair/replication) were allowed to mate with the opposite sex of each treatment individuals. Each individual pair was reared in a plastic container with a white paper and top covered with muslin cloth. Adults were provided with a 10% pure honey solution which was renewed every 2 days. Observations were recorded for 24 h of time on the number of pairs that could mate successfully in each container and also the adult development period. In each container, presence or absence of egg mass, the total number of eggs laid and the number of larvae that subsequently hatched out of the eggs were recorded. The first 100 larvae to be hatched were reared individually to record viral mortality of the progeny larvae. Where the cause of death was not clear, the larval extracts were smeared onto a microscope slide, and viewed under a light microscope for OBs. Finally, the effect of different concentrations on progeny mortality was recorded in F1 generation.

Statistical analysis

All data were analyzed and checked for normal distributions. Data on development period and reproductive abilities were subjected to ANOVA, followed by Tukey's post hoc test for comparison of mean values. All data on percentage were subjected to arcsine square root transformation prior to ANOVA. All statistical analyses were carried out using computer software IBM SPSS-25.

Results

The study was very particular in evaluating the effect of different concentrations of SpfrNPV on larval and pupal development rates, adult emergence, egg production and egg hatchability in the surviving larval population. The SpfrNPV was used in this study and had divided the larvae into six different groups in which varying concentrations of SpfrNPV were administered through diet

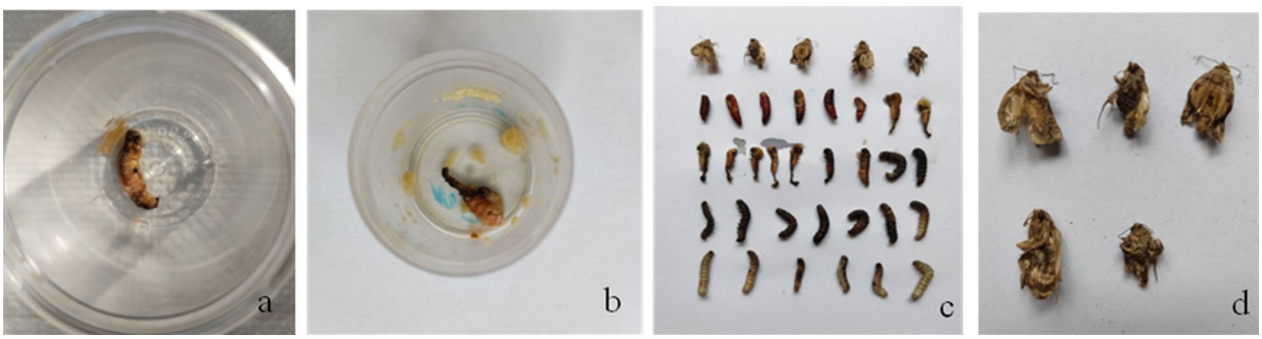

Fig. 1 **a** Liquification from 5th instar larva of *Spodoptera frugiperda*. **b** Molting defects in SpfrNPV infected *S. frugiperda* larva. **c** Mortality observed in 4th and 5th instar *S. frugiperda* larvae, pre-pupae, pupa due to SpfrNPV infection. **d** Deformation in wings, antennae and abdomen of adult moths of *S. frugiperda* due to SpfrNPV infection

ranging from 10^4 OB/ml to 10^7 OB/ml. The larvae in all the different concentrations exhibited the characteristic baculoviral infection symptoms like change of larval body color and appearance from normal color to puffy and milky white, liquefaction in late 5th larval instar and in pupal stage (Fig. 1). Those larvae which did not show these characteristic symptoms were smeared and viewed under a phase contrast light microscope (× 400) for the presence of OBs of SpfrNPV.

Larval and pupal developmental rates

Duration of mean developmental periods of infected 3rd and 4th larval instars was significantly higher ($F=2.945$; $F=18.414$; $df=5, 20$; $P<0.05$) in SpfrNPV infected larvae than the control at all tested viral concentrations (Table 1). Pre-pupal duration was also higher in the infected group in all viral concentrations than the control ($F=2.580$; $P=0.051$) (Table 1). Additionally, a very high mortality rate was observed in infected pupae in a concentration dependent fashion. The percentage of pupal mortality rate ranged from 40.74 to 72.73% in the lowest and highest concentration of SpfrNPV, respectively. Developmental period of male pupae was found to be significantly longer in infected groups than to the uninfected ones. However, a similar correlation was not observed in infected and control female pupae. Infected pupae of both sexes showed a significant loss in weight in infected group as compared to the control (Table 2). Overall, the effect of indigenous strain of SpfrNPV was much pronounced at the pupal stage with higher mortality and weight loss than that seen at the larval stage.

Table 1 Effect of different concentrations of SpfrNPV on the development stages (mean ± SE) of *Spodoptera frugiperda*

	Concentration (OBs/larva)	Days			
		3rd instar	4th instar	5th instar	Pre pupae
1	1.20×10^7 (n = 45)	3.42 ± 0.20^{ab}	3.05 ± 0.12^{b}	1.68 ± 0.24^{c}	2.98 ± 0.17^{b}
2	2.83×10^6 (n = 46)	3.72 ± 0.19^{a}	3.20 ± 0.12^{b}	1.84 ± 0.27^{bc}	2.27 ± 0.06^{ab}
3	2.00×10^6 (n = 46)	3.56 ± 0.22^{ab}	3.16 ± 0.05^{b}	2.16 ± 0.29^{abc}	2.58 ± 0.22^{ab}
4	1.29×10^5 (n = 47)	3.84 ± 0.16^{a}	4.38 ± 0.29^{a}	2.68 ± 0.21^{abc}	2.38 ± 0.37^{ab}
5	5.69×10^4 (n = 47)	3.50 ± 0.33^{ab}	3.39 ± 0.17^{b}	2.78 ± 0.16^{ab}	2.32 ± 0.05^{ab}
6	Control (n = 49)	2.74 ± 0.17^{b}	2.24 ± 0.06^{c}	3.06 ± 0.14^{a}	2.05 ± 0.10^{a}

Within columns, mean number of days followed by the same letter do not differ significantly [ANOVA, Tukey's HSD; $P<0.01$]

Biological attributes of adults

Adults emerging from different batches were observed for morphological defects. A large percentage of infected adult moths exhibited wing deformities, while antennal and abdominal defects were also readily visible (Fig. 1). Longevity in adult moths of both sexes was monitored in the surviving populations of both control and infected groups (Table 2). The infected adults had significantly reduced longevity in both males ($F=6.273$; $P=0.002$) and females ($F=13.652$; $P=0.001$). The effect was observed more at the highest concentration of SpfrNPV (T1 and T2). Infected male and female moths, which did not display apparent morphological defects, were recorded. Upon comparison with control pairs, a substantial impact on fertility of infected pairs in a concentration dependent manner was observed. In infected groups, infertile adult pairs in a dose dependent fashion as opposed to the control groups where all pairings lead to offspring were observed (Table 3). Further, the mates of virus-treated adults showed highly reduced egg production ($F=31.255$; $P<0.05$), ranged from 150.03 to 338.33 at a level of 30–70% than the control. The larvae emerging from the eggs ranged from 71.11 to 227.89 ($F=74.520$; $P<0.05$), which was again significantly lower than the control (Table 3). The percentage of egg

Table 2 Debilitating effect of different concentrations of SpfrNPV on pupal period, pupal weight and adult longevity (mean ± SE) of *Spodoptera frugiperda*

Treatments	Concentrations	Pupal period (days)		Total percent of pupal mortality	Weight of Pupae (mg)		Adult longevity	
		Female	Male		Female	Male	Female	Male
T1	1.20×10^7	11.99 ± 0.40^{a}	11.33 ± 0.65^{a}	72.73	164.44 ± 4.84^{b}	188.89 ± 2.22^{ab}	3.50 ± 0.64^{c}	3.50 ± 0.86^{b}
T2	2.83×10^6	11.48 ± 0.47^{ab}	10.88 ± 0.69^{ab}	62.06	153.89 ± 7.22^{b}	165.33 ± 1.33^{ab}	4.25 ± 0.47^{c}	3.71 ± 0.47^{b}
T3	2.00×10^6	9.81 ± 0.50^{b}	9.48 ± 0.55^{ab}	62.50	170.22 ± 1.93^{b}	175.55 ± 9.49^{ab}	5.50 ± 0.28^{bc}	4.00 ± 0.70^{b}
T4	1.29×10^5	10.94 ± 0.34^{ab}	10.94 ± 0.34^{ab}	55.17	157.77 ± 8.01^{b}	139.22 ± 9.33^{b}	5.75 ± 0.62^{bc}	5.51 ± 0.64^{ab}
T5	5.69×10^4	11.41 ± 0.62^{ab}	10.21 ± 0.34^{ab}	40.74	149.99 ± 8.81^{ab}	167.77 ± 22.79^{ab}	7.00 ± 0.70^{ab}	5.67 ± 0.62^{ab}
T6	Control	11.50 ± 0.46^{ab}	9.01 ± 0.38^{b}	8.10	202.42 ± 9.87^{a}	201.11 ± 11^{a}	9.25 ± 0.40^{a}	7.75 ± 0.47^{a}

Within columns, means followed by the same letter do not differ significantly [ANOVA, Tukey's HSD; $P<0.01$]

Table 3 Debilitating effect of different concentrations of SpfrNPV on fertility and fecundity and their effect were observed on the F1 generation (viz, number of eggs and number of larvae (mean ± SE) hatched

	Concentration	Percentage of infertile adults	Total number of eggs	Total number of larvae	Percentage of larvae survived
1	1.20×10^7 ($n=6$)	33.3	150.03 ± 10.91^c	71.11 ± 7.46^d	4
2	2.83×10^6 ($n=6$)	33.3	340.04 ± 15.49^b	140.33 ± 17.89^c	16
3	2.00×10^6 ($n=6$)	16.6	312.89 ± 20.46^b	$179.11 \pm 12.74b^c$	23
4	1.29×10^5 ($n=6$)	0	297.66 ± 20.30^b	171.89 ± 3.82^{bc}	42
5	5.69×10^4 ($n=6$)	0	338.33 ± 28.59^b	227.89 ± 11.38^b	65
6	Control ($n=6$)	0	474.55 ± 8.26^a	405.33 ± 18.80^a	92

Within columns, means followed by the same letter do not differ significantly [ANOVA, Tukey's HSD; $P<0.01$]

hatching ranged from 47.40 to 67.36%. The highest concentration of SpfrNPV such as T1 and T2 was associated with less than 50% of egg hatching. The results suggested that this indigenous strain of SpfrNPV had a high potential in reducing the pest incidence in subsequent generation in the surviving populations of the infected larvae.

Discussion

Baculoviruses have been extensively utilized for their ability to cause mortality of larvae in several lepidopteran crop pests; however, their sub-lethal effects on the pest population are frequently ignored. Though a number of studies have been investigated and analyzed the debilitating effects associated with baculoviral infections, the severity of the observed effects appeared to be partly influenced by the species or strain of the infecting baculovirus (Akhanaev et al. 2020). Limited studies have monitored the effect of *S. frugiperda* nucleopolyhedrovirus on surviving populations of the FAW (Zakseski et al. 2021). In this regard, the sub-lethal effects of indigenous strain of SpfrNPV isolated from Chikkaballapura district, Karnataka on FAW population, in India, was observed. Different concentrations of SpfrNPV on late second instar larvae of *S. frugiperda* were tested and recorded on several larval, pupal and adult parameters. The study on SpfrNPV, an overall increase in development period during larval and pupal stages in infected populations with respect to control was observed. An increase in larval and pupal developmental time after baculovirus infection is a commonly observed response in a number of other baculoviral species as well (Cabodevilla et al. 2011). A high mortality rate at the pupal stage with characteristic symptoms like oozing of fluid and liquefaction in infected organisms was observed. The weight of the infected male and female pupae was significantly lower than the healthy pupae maintained under control treatment. However, there were conflicting results regarding the effect of baculovirus infection on the pupal weight of infected insects. While several studies have reported a similar decrease in pupal weight (Cabodevilla et al. 2011), there are others which have not observed the reduction in weight after infection (Führ et al. 2021). The effect seems to be dependent on the strain or species of the baculovirus and not on the baculoviral load or the stage of the infected insect. Significant reduction in pupal weight at all the tested concentrations of baculoviral infection was recorded. Moreover from related studies, there is no correlation between the reduction of pupal weight and the stage at which the insect was infected.

Effects of sub-lethal infection of baculovirus on fertility and fecundity were studied in more details than development and there are numerous reports of reduction in oviposition rate or fecundity (Patil et al. 1989). In this study, the highest concentration of SpfrNPV was associated with infertile adults and low fecundity. In all the treatments, several adults were deformed with crippled wings and/or distorted abdomens.

The present findings suggest that the baculoviral infection has a profound effect on growth and development of surviving insects and there is a marked reduction in fertility and fecundity in the infected adults. Some insects surviving after the virus treatment are likely to be covertly infected due to the consumption of viral OBs and a portion of those survivors may transmit the virus vertically. Vertical transmission accompanied by subsequent horizontal transmission of baculoviruses will help to reduce the pest population naturally. This study has the base line capability for identification of different strains in the local field system for vertical transmission. Moreover, SpfrNPV strain needs to be evaluated under field for its effect on population suppression, which will provide an additional profit for the small land holding farmers as a biological control strategy for FAW management.

Conclusion

The triggering of sub-lethal diseases and initiating viral epizootics could improve further the effectiveness and help the farmers to reduce the cost of baculovirus-based control methods. This area of study opens widespread

perspectives for use in plant protection, especially against the insect pests which have a migratory activity.

Abbreviations

NBAIR	National Bureau of Agricultural Insect Resources
SpfrNPV	*Spodoptera frugiperda* Nucleopolyhedrovirus
ICAR	Indian Agricultural Research Institute
LC50	Sub-lethal concentration
v/v	Volume per volume

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Author contributions
DO, RKP, AG, VT, MM, NN and SG designed and executed the experiments and carried out the study. DO, NN, AG and RKP wrote the manuscript. DO, SG, MM, and VT analyzed the data. All authors read and approved the final manuscript.

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Availability of data and materials
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Declarations

Ethics approval and consent to participate
Not applicable.

Consent for publication
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Competing interests
The authors declare that they have no competing interests.

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