Comunicata Scientiae
Horticultural Journal

ORIGINAL ARTICLE
published: 14 March 2021
https://doi.org/10.14295/CS.v12.3424

Analysis of baculovirus spodoptera virulence in fall armyworm fed with cassava leaves

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Abstract

The fall armyworm, *Spodoptera frugiperda* (JE Smith, 1797) (Lepidoptera: Noctuidae) is considered the main pest of corn (*Zea mays* L.) in Brazil and feeds on several other plant species, including cassava (*Manihot esculenta* Crantz). The food substrate influences the control efficiency of baculovirus and there aren't studies on the effects of the application of baculovirus *Spodoptera frugiperda multiple nucleopolyhedrovirus* (SfMNPV) on cassava leaves in the mortality of *S. frugiperda* larvae. The main objectives of this study were to evaluate the efficiency of SfMNPV isolate 6 on *S. frugiperda* larvae fed on corn and cassava leaves. The food substrates were treated with three baculovirus concentrations (2×10^5, 2×10^6 and 2×10^7 OB mL^{-1}) of a semipurified suspension, and of a commercial formulation (CartuchoVit®), both containing SfMNPV isolate 6, and then were offer to *S. frugiperda* second instar larvae. The semipurified virus was more virulent than the commercial formulation, regardless of the food substrate provided to insects, when concentrations of 2×10^5 and 2×10^6 OB mL^{-1} were used. However, there was no difference between treatments when baculovirus suspension of 2×10^7 OB mL^{-1} was use and the mortality rates were higher than 91%. The mortality was higher when the larvae fed on cassava leaves treated with SfMNPV. Therefore, the food substrate increased the efficiency of SfMNPV, which promises the use of this virus in the management of *S. frugiperda* in cassava crops.

Keywords: Baculoviridae, entomopathogen, *Manihot esculenta*, biological control

Introduction

Spodoptera frugiperda (JE Smith, 1797) (Lepidoptera: Noctuidae), the fall armyworm, is the main corn pest in Brazil and a cosmopolitan insect that attacks several plant species, for example, soybean, cotton, bean, castor bean, sorghum, sugar and millet (Valicente et al., 2013; Silva et al., 2018; Chormule et al., 2019). The availability of alternative hosts throughout the year favors the occurrence of this pest and makes management difficult (Barros et al., 2010; Machado et al., 2014).

Among the agricultural crops, cassava (*Manihot esculenta* Crantz) (Euphorbiaceae) and corn (*Zea mays* L.) (Poaceae) stand out in Brazil for their socioeconomic importance, whether in human or animal nutrition (Machado et al., 2014). Despite the occurence of *S. frugiperda* in several plant species, maize is one of the preferred hosts (Boregas et al., 2013), although cassava also provide the nutritional requirements of this pest (Lopes et al., 2008).

Farmers plant maize and cassava together (Ferreira et al., 2014; Silva et al., 2016). Therefore, the incidence of *S. frugiperda* in corn may affect cassava (Machado et al., 2014) and cause losses, because as defoliants and due to voracity, the caterpillar can cause defoliation levels beyond the tolerance capacity of the host plant (Moscardi et al., 2012).

Baculoviruses can be used in integrated pest management programs due to their natural occurrence and host specificity, with low impact on beneficial insects and vertebrates (Barrera et al., 2011; Haase et al., 2015; Lacey et al., 2015). Moreover, the baculovirus use is compatible with the use of transgenic plants, with cultural control methods and with chemical control (Valicente, 2015).

The food substrate influences the infectivity of baculoviruses in the hosts (Cory & Hoover, 2006; Elderd,

Received: 20 May 2020
Accepted: 10 October 2020

2019). Substances present on the leaf surface of some plant species or released in the insect's intestinal lumen, during digestion, may inactivate or reduce the efficiency of baculoviruses or may increase the sloughing of the regions where primary infections occur in the midgut cells (Hoover et al., 2000; Lasa et al., 2018).

The pathogenicity and virulence to *S. frugiperda* of *Spodoptera frugiperda multiple nucleopolyhedrovirus* (SfMNPV), popularly known as baculovirus spodoptera, were evaluated and confirmed in corn crops. However, the effect of this virus has been little studied on larvae that consumed other food, as was done, in the laboratory, for larvae fed with artificial diet, castor bean leaves, soybean, cotton, bean, sorghum and millet (Valicente et al., 2013; Silva et al., 2018). There aren't studies that show whether the SfMNPV baculovirus is efficient to control *S. frugiperda* larvae when fed on cassava leaves.

The objective was to evaluate the efficiency of an SfMNPV isolate, on *S. frugiperda* larvae fed with cassava leaves, under laboratory conditions.

Material and Methods

The experiments were conducted at the Center for Scientific and Technological Development in Phytosanitary Management of Pests and Diseases (NUDEMAFI) of the Center for Agricultural Sciences and Engineering at the Federal University of Espírito Santo, located in Alegre, Espírito Santo State, Brazil.

Artificial rearing of Spodoptera frugiperda

The artificial rearing of *S. frugiperda* larvae was carried out in a room, temperature of 25 ± 2 °C, and relative humidity of 60%, and a photophase of 12 hours. Adults were kept in PVC cages, fed with a 10% honey solution soaked in cotton. Sheets of white paper covering the internal part of the cage were used as a substrate for oviposition, being removed every two days to collect the egg masses, which were kept in 1L transparent plastic recipients until the larvae hatched. The newly hatched larvae were transferred with the aid of a soft brush to a 100 mL plastic recipients, and when they were 5 days old fifty larvae were transferred to acrylic boxes (dimensions of 11 x 11 x 3 cm), and when they were 10 days old were individualized in acrylic recipients (3 cm in diameter x 1.5 cm in height), until pupal stage. Larvae were fed on modified artificial diet (without the addition of an inhibitory solution and replacing agar with carrageenan) (Cruz, 2000), provided ad libitum. The pupae were collected and kept in acrylic boxes (gerbox) until they were transferred to the breeding cages, restarting the cycle.

Multiplication of the SfMNPV virus

Isolate 6 of SfMNPV from the Laboratory of Biological Control of Embrapa Maize and Sorghum, which causes high mortality and doesn't cause liquefaction of the integument immediately after larvae death (Vieira et al., 2012; Valicente et al., 2013). Virus multiplication was performed *in vivo* and the inoculation was done by offering artificial diet previously sprayed with a baculovirus suspension containing 1 x 10^8 occlusion bodies (OBs) mL^{-1}. The diet was left to dry for 30 minutes and transferred, to 250 mL rectangular plastic recipients. Larvae were individualized after 48 hours, in 50 mL plastic (type of coffee) recipients with artificial diet, without viruses and made with the addition of formaldehyde (40% v v^{-1}) (Cruz, 2000), and closed with an acrylic lid. Subsequently, dead larvae with symptoms of virus infection were macerated in 1% SDS (Sodium Dodecyl Sulfate) buffer. The macerate was later filtered through a layer of cheesecloth to remove fatty tissues and the denser parts of larvae, such as a cephalic capsule (Hashimoto et al., 2000). The filtrate viral suspension was centrifuged three times, in a 1% SDS buffer at 6,000 rpm for 20 minutes. The pellet was resuspended in sterile distilled water, with a vortex, and frozen until use.

Bioassay

S. frugiperda larvae of second instar (4 days old), were taken of the artificial rearing mentioned above, were fed with cassava leaves (cultivar Cacau Branco) and corn (Semeali®, hybrid XB 4013) and viral suspensions in the concentrations of 2 x 10^5, 2 x 10^6 and 2 x 10^7 OB mL^{-1}, representing applications of a low concentration, the concentration recommended by the manufacturer and a high concentration of the product, respectively.

The viral suspensions were prepared with distilled water using semipurified isolate 6 and the commercial formulation CartuchoVit® (product based on SfMNPV, formulated as wettable powder), plus 250 μL (0.05% v v^{-1}) of the non-ionic surfactant Tween 20 (Polysorbate 20). Control treatment consisted only of distilled water and surfactant.

The inoculation was done by submerging corn and cassava leaves in 500 mL of the viral suspensions for 30 seconds. The leaves were placed on filter paper for about ten minutes, to remove the excess of water from the leaves. The pieces of leaves were placed in a 250 mL plastic recipient, arranged to cover the total bottom of the recipient and offered *ad libitum* to *S. frugiperda* larvae of second instar (4 days old). Each recipient received 12 larvae that were kept in a chamber at 25 ± 2 °C for 48 hours. Larvae were individualized in 50 mL plastic

recipients containing an artificial diet, after the period of viral inoculation and kept in a room at 25 ± 2 °C.

The experimental design was a completely randomized and a 3 x 2 x 2 factorial, with four replications, where the treatments consisted of the combinations between the three concentrations of viral suspensions, the two food substrates, maize and cassava leaves, and the two viruses formulations, pure and commercial. Larval mortality was checked daily, until the pupal stage and it was assessed by the formula: percentage of mortality = number of dead larvae with virus symptoms / (number of dead larvae with virus symptoms + number of pupae). Control data were used to determined correct mortality of virus treatments by Abboott's formula (Abbott, 1925).

The Shapiro-Wilk test proved the normal distribution of waste. The mortality data were subjected to analysis of variance (ANOVA) and test of Tukey, at a level of 5% probability. Survival analysis was performed using Kaplan-Meier non-parametric test, in which time zero was considered as the date that the *S. frugiperda* larvae were exposed to the SfMNPV. The statistical software R 3.5.2 (ExpDes.pt, survival and surviminer packages) (R Core Team, 2020) was used to perform the statistical analyzes.

Results

There was no triple interaction among the factors food substrate, type of virus, isolated 6 semipurified or comercial CartuchoVit®, and concentration (F = 1.44; *p* = 0.250), but there was a combination of the type of virus with the concentrations of virus suspensions (F = 46.16; *p* <0.001), and significant effect of the food substrate (F = 32.43; *p* <0.001).

Semipurified isolate 6 of SfMNPV was more virulent than the commercial formulation when compared in the concentrations of 2 x 10^5 and 2 x 10^6 OB mL^{-1} and didn't differ when compared in the concentration of 2 x 10^7 OB mL^{-1}, regardless of the food substrate tested (Figure 1). Considering the concentration levels, within each level of the virus used, when the virus was applied at a concentration of 2 x 10^5 OB mL^{-1}, mortality of *S. frugiperda* larvae was lower than when the virus was applied in the other concentrations, those that didn't differ from each other, regardless of whether the virus applied was the semipurified or the commercial formulated CartuchoVit® (Figure 1).

The mean survival time of *S. frugiperda* larvae was inversely proportional to the concentration of the applied baculovirus suspension, regardless of the food substrate tested (Figure 2).

Considering the simple effect of the food substrate, mortality was higher when the larvae fed on cassava leaves treated with SfMNPV when compared to those that fed on corn leaves (Figure 3). However, there was no difference between the survival time of *S. frugiperda* larvae when diferente food substrate were tested (Figure 4).

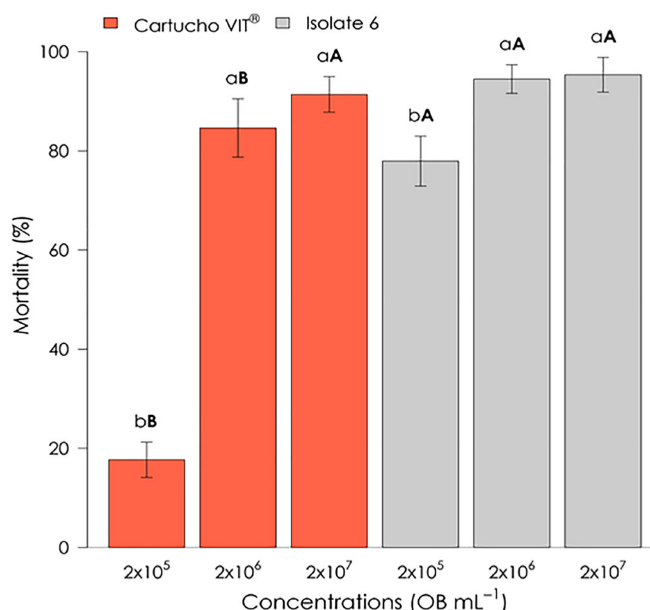

Figure 1. Effects of the type of baculovirus (semipurified isolate 6 or commercial CartuchoVit®), and the concentration of the baculovirus suspension on the mortality of second instar *S. frugiperda* larvae. Means followed by the same letter, lower case between the different concentrations within each type of formulated applied and upper case between types of formulated baculovirus applied within the same concentration, do not differ by 5% probability by the Tukey test.

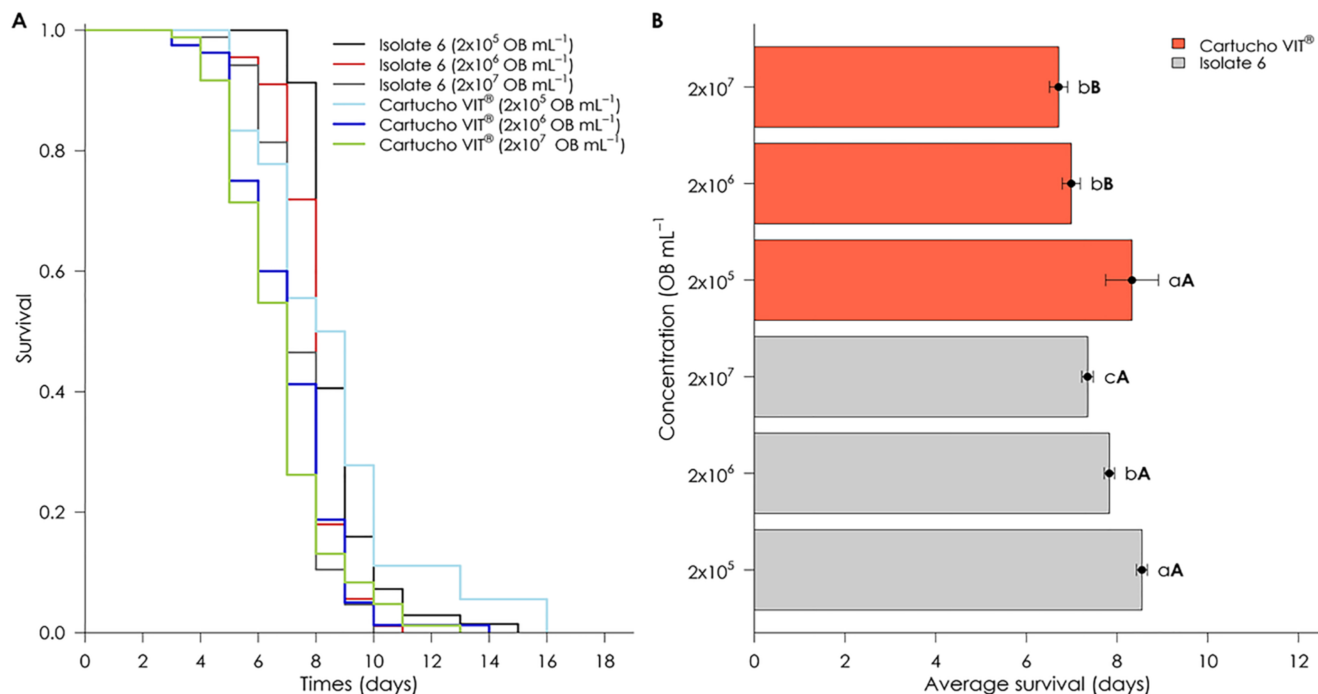

Figure 2. Analysis of survival (A) and average survival time (B) for the effects of the type of virus and the concentration of baculovirus suspension on second instar *S. frugiperda* larvae. Averages followed by the same letter, lower case between the different concentrations within each type of formulated applied and upper case between types of formulated applied within the same concentration, do not differ by 5% probability by the log-rank test.

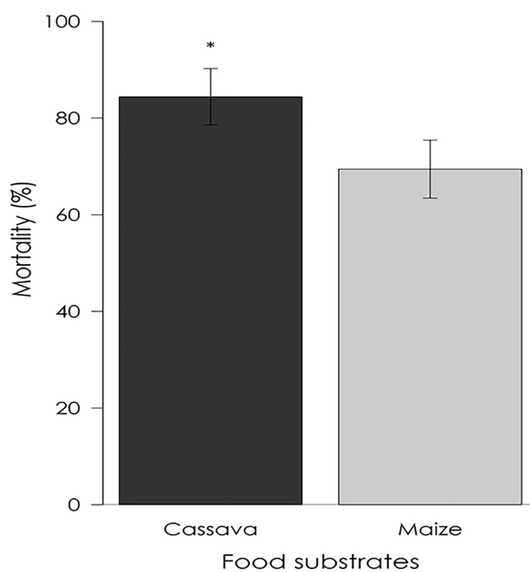

Figure 3. Effects of the food substrate treated with the SfMNPV on second instar *S. frugiperda* mortality.
* Significant at 5% level of probability by the F test.

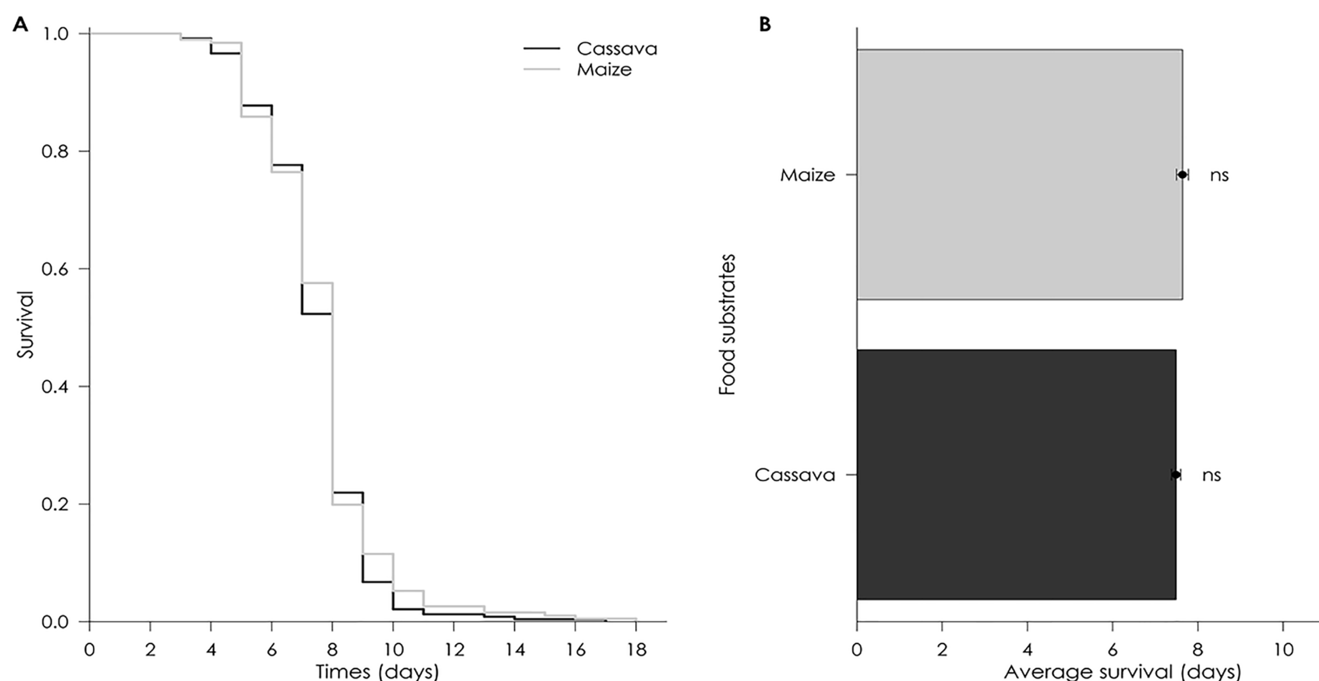

Figure 4. Analysis of survival (A) and mean survival time (B) for the effect of the food substrate treated with the SfMNPV virus on second instar *S. frugiperda* larvae. [ns] Not significant at the 5% probability level by the log-rank test.

Discussion

The baculovirus infection begins when there are occlusion bodies (OBs) on the leaf surface that are ingested by the larvae. The alkaline pH of the larvae's midgut dissolve the OBs releasing the virions, called occlusion-derived virus (ODVs), which bind to and infect the epithelial cells of the midgut after crossing the peritrophic membrane (PM). Infected intestinal cells produce a second virus phenotype, the budded virus (BV), which causes systemic infection (Harrison & Hoover 2012). The defense mechanisms of insects against baculovirus infection involve the ability to block the PM against infection (Wang & Granados 1998), the sloughing and apoptosis of infected cells of the intestinal epithelium (Hoover et al., 2000; Dougherty et al., 2006). The efficiency of viral infection is influenced by the type of baculovirus-based formulation (Behle & Popham, 2012). This explains the difference between the pure and the commercial virus.

The increase in the concentration of virus makes it difficult to the hosts defense and increases mortality, since PM has a limited capacity to act as a protective filter (Mohan et al., 2006), and when the concentration of virus is higher in the lumen, the possibility that viral particles will overcome this barrier represented by PM has increased.

Probably, if the number of foci of primary infection is increased, the release of BV will be higher, accelerating the occurrence of secondary infection and, consequently, the average survival time of the larvae will be reduced. This contributes to the reduction in the lethal time due to the increase in applied viral concentration (Tang et al., 2011), and this corroborates with the results found in this study.

The food substrate influences in several ways the success of the infection caused by baculovirus, and the consumption of the foliage of the host plant may increase the larval resistance to baculovirus or improve the performance of insect pathogens (Cory & Hoover, 2006; Elderd, 2019). In addition, substances present in the ingested food can influence the thickness of the PM, which is an important barrier against the entry of baculoviruses in the host cells (Plymale et al., 2008).

The integrity of the PM that lines the midgut can be compromised by interactions with phytochemicals and plant enzymes, such as secondary defense metabolites of the ingested plant that can cause narrowing down, or damage to this membrane, which facilitates the invasion of ODVs in the basal cells of the medium intestine of the host insect, accelerating the progress of the primary infection (Pechan et al., 2002). For example, the consumption of corn plants producing a protease induced by phytophagous insects has damaged PM (Pechan et al., 2002). In the case of this work, cassava is a cyanogenic species with natural occurrence of the glycosides linamarin, lotaustralina and that the levels of hydrocyanic acid (HCN) vary between parts of the plant, with high levels of HCN in cassava leaves (Oliveira et

al., 2012). However, the effects of these substances on the integrity and physical properties of *S. frudiperda* PM aren't yet known.

The nutritional quality of the ingested plant can affect different indicators of the host insect's immune function, including the number of hemocytes, the levels of phenoloxidase and the encapsulation responses (Klemola et al., 2007; Shikano et al., 2010). Insects that eat low-quality plants seem to be at higher risk of baculovirus infection compared to those that eat high-quality plants (Shikano et al., 2010) and the biological parameters of *S. frugiperda* were better when the larvae fed on corn leaves instead of cassava leaves, showing that the corn plant is a food of better nutritional quality and that *S. frugiperda* is more adapted to this plant, in relation to the cassava plant (Machado et al., 2014).

In addition, phytochemicals or phytochemical-induced signals, can cross the intestine and modify the host's immune function or physiology, resulting in an increase or decrease in susceptibility to baculovirus disease in relation to plant quality (Klemola et al., 2007; Shikano et al., 2010). The lower nutritional quality of cassava leaves as food for the growth and development of *S. frugiperda* larvae may have caused the larvae to eat more, with a compensatory effect and, consequently, a greater intake of viruses. There is also the possibility that metabolites present on the cassava leaf surface or released in the intestine of larvae during the digestion process may delay the development of *S. frugiperda* larvae and thus increase the period of vulnerability of this pest to SfMNPV. The increasing resistance within and between larval stages to baculoviruses is called developmental resistance (Hoover et al., 2002; Grove & Hoover, 2007). Interspecific and intraspecific qualitative differences between plants can influence larval growth rates and mechanisms of physical and immunological resistance (Lampert, 2012; Shikano, 2017; Shikano et al., 2017).

Plants have a wide range of herbivory-induced defenses (Agrawal, 2011), but many of these defenses aren't immediately lethal, but they reduce the development of herbivores (Shikano et al., 2018). The hypothesis of high mortality and slow growth deals with how sublethal plant defense indirectly increases the period of vulnerability of herbivores to natural enemies (Moran & Hamilton, 1980; Shikano et al., 2018). Since the susceptibility of larvae to baculoviruses is strongly dependent on the stage of development, it seems likely that the growth retardation of the larvae, mediated by the plant, would keep the larvae susceptible for longer (Shikano et al., 2018). For example, the anti-herbivory defenses induced by soybean plants, *Glycine max* (L.) Merrill, inhibit the growth of *S. frugiperda* larvae and increase their susceptibility to the SfMNPV baculovirus (Myers & Cory, 2016), consistent with the hypothesis of slow growth and high mortality (Shikano et al., 2018).

Despite the promising results, the use of SfMNPV for the control of *S. frugiperda* larvae in cassava crops should be studied in the field, as several environmental factors influence the viability of viruses and the infection process, before a recommendation to producers the effects of these interactions and the effectiveness of this control method must be known.

Conclusions

The baculovirus SfMNPV is efficient to control *S. frugiperda* larvae fed with cassava leaves, under laboratory conditions.

Acknowledgments

This work was carried out with the support of the National Council for Scientific and Technological Development (CNPq) and the Espírito Santo Research and Innovation Support Foundation (Fapes). To Paulo Bittar, owner-partner of Vitae Rural group for the kindness of providing the commercial formulation that was used in this work.

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Conflict of Interest Statement: The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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