Developing a biocontrol strategy to protect stored potato tubers from infestation with potato tuber moth species in the Andean region

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ORIGINAL CONTRIBUTION

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Funding information
German Academic Exchange Service (DAAD)

Abstract
Heavy infestations of stored potato (Solanum tuberosum L.) tubers by the two potato tuber moth species Symmetrischema tangolias (Gyen) and Tecia solanivora (Povolny) frequently occur in Andean potato-growing regions of Ecuador. The aim of the study was to develop a biological control strategy for both species using powder formulations made of inert substances, Phthorimaea operculella (Zeller) granulovirus (PhopGV) and Bacillus thuringiensis Berliner subsp. kurstaki (Btk). The LC50 of PhopGV on T. solanivora was 0.33 LE/L, and Btk caused 82.7% mortality at a concentration of 100 g/L in bioassays. The efficacy of talcum, kaolin, calcium carbonate and sand ranged between 76.2% and 98.7%. Calcium carbonate was highly effective to control both species; however, its efficacy was affected by the relative humidity and dropped to 55.4% at relative humidity of 100%. PhopGV at concentrations of five larvae equivalents (LE) per kg kaolin and Btk at a concentration of 60 g Btk/kg talcum caused 95.7% and 88.1% mortality of T. solanivora, respectively. In storage experiments, the efficacy of calcium carbonate alone and in combination with PhopGV (20 LE/kg) and Btk (15 g/kg) caused 95.0–99.8% mortality of T. solanivora in all treatments and reduced infestation on potato tubers by 83.6%–91.0%. In the case of S. tangolias, Btk significantly increased mortality to 96.5% compared with calcium carbonate alone and reduced tuber infestation by 83.4%. Storage of potato tubers in thin layers enhanced the efficacy of the calcium carbonate treatment compared with storage in bags. It was concluded that calcium carbonate alone seems to be appropriate for the control of T. solanivora, and an addition of 15 g Btk/kg would improve the control of S. tangolias. It is suggested to test these new formulations under on-farm storage conditions.

KEYWORDS
Bacillus thuringiensis, granulovirus, inert substances, Phthorimaea operculella, Symmetrischema tangolias, Tecia solanivora

1 | INTRODUCTION

The potato tuber moths Tecia solanivora (Povolny), Symmetrischema tangolias (Gyen) and Phthorimaea operculella (Zeller) [Lepidoptera, Gelechiidae] are important storage pests of potato (Solanum tuberosum L.) in the Andean region. Infestations in stores start mostly through freshly harvested infested tubers or through moths entering storage facilities. Larval mining in tubers makes them unsuitable for consumption, and damage increases quickly when several generations develop during the storage period. Complete destruction of stored potato tubers has
been reported (Hilje, 1994; Palacios & Cisneros, 1997; Pollet, Barragán, & Zeddam, 2003). The importance of the three moth species varies regionally. In Andean potato stores, *P. operculella* is less prevalent than *S. tangolias* in Bolivia and Peru (Calderón, Crespo, Lino, Carvajal, & Herbas, 2002; Keller, 2003) or *T. solanivora* in Costa Rica and Ecuador (Gómez-Bonilla, López-Ferber, Caballero, Léry, & Muñoz, 2012; B. Schaub, personal observation). This can be explained by the fact that *P. operculella* is less adapted to the cool temperature conditions in the Andean potato-growing zones than are *T. solanivora* and *S. tangolias* (Dangles, Carpio, Barragán, Zeddam, & Silvain, 2008; Kroschel & Schaub, 2013; Sporleder, Schaub, Aldana, & Kroschel, 2017). *Tecia solanivora* is considered the most serious pest in potato storages in its area of distribution from Central America to Ecuador (Barragán et al., 2002; Carrillo & Torrado-León, 2013; Palacios, Sotelo, & Saenz, 1997). *Symmetriscchema tangolias* is a serious pest in Bolivian and Peruvian potato storages (Calderón et al. 2002; Keller, 2003); in Central Ecuador, heavy infestation in storage has also been observed. In the Carchi province of Ecuador, however, high numbers of *S. tangolias* adults had been caught in pheromone traps in the field, but potato storages were infested by *T. solanivora* and *P. operculella* only (Suquillo, Rodríguez, López, & Sevillano, 2011a). Likewise, in parts of Central Ecuador, where high numbers of *S. tangolias* adults had been also observed in pheromone traps, potato storages were only infested by *T. solanivora* (B. Schaub, personal observation).

Potato tubers destined for commercial use are sold within a few days after harvest (Alacrón & Echavarría, 2002; Devaux, Ordinola, Hibon, & Flores, 2010). Only potato tubers intended for own consumption and seed stored by farmers need to be protected from potato tuber moth infestation. The duration of the storage period varies with regard to the potato-growing seasons of the different potato production regions. In some regions, potato is sown year around. In others, cropping is restricted by temperature or rainfall conditions to one or two seasons per year; in which case, storage periods can last up to 4 months and more. Seed tubers need to be stored for approximately 3 months after harvest until dormancy is broken and tubers are sprouting. For the protection of stored tubers against *P. operculella* infestations, dust formulations have been developed based on *P. operculella* granulovirus (PhopGV) or *Bacillus thuringiensis* subsp. *kurstaki* (Btk) as active ingredients that act on neonate larvae entering potato tubers (Kroschel & Koch, 1996; Lacey & Kroschel, 2009). PhopGV has been isolated from *P. operculella* larvae in many countries all over the world (Kroschel, Fritsch, & Huber, 1996; Sporleder, 2003). It infects *P. operculella* larvae, which die 10–14 days after oral uptake. It was also isolated from *T. solanivora* in Venezuela (Niño, 1996), Colombia (Villamizar et al., 2008), Ecuador (Zeddam et al., 2005) and Costa Rica (Gómez-Bonilla, López-Ferber, Caballero, Léry, & Muñoz, 2011). Dust formulations are commercially produced for the protection of stored seed tubers from *P. operculella* infestation in Peru, Bolivia, Tunisia and Egypt (Sporleder & Kroschel, 2008). In Ecuador and Colombia, semi-industrially produced PhopGV formulations were evaluated against *T. solanivora* in potato stores and reduced infestation by 90%–100% (Sotelo, Palacios, & Lagnaou, 2004; Suquillo, Rodríguez, López, & Gallegos, 2011b). Btk formulations protected potato tubers against *S. tangolias* infestation for approximately 3 months (Mamani, 2008).

Symmetriscchema tangolias is not susceptible to PhopGV, but *T. solanivora* is to some degree susceptible to Btk (Pérez, Rodríguez, & Cotes, 1997). A formulation that contains the two active ingredients is likely to protect potato tubers against both pest species. On the other hand, inert substances, such as kaolin and talcum, used for the formulation of the PhopGV or Btk products are efficient against the potato tuber moth species even without the addition of the active ingredients (Carpio, 2008; Kroschel & Koch, 1996; Mamani, Sporleder, & Kroschel, 2011; Niño & Notz, 2000). The use of inert substances would have several advantages over biopesticide formulations (e.g., better availability, cheaper price); however, efficacy of inert substances is not consistent.

This study aimed to investigate the potential of inert substances for control of *T. solanivora* and *S. tangolias* under simulated storage conditions and to compare the impact of different storage methods. As efficacy of inert substances alone might not be sufficient for all potato tuber moth species, biopesticide formulations containing PhopGV and Btk were also evaluated in bioassays and storage experiments to identify a biopesticide formulation for protection of stored potato tubers against infestations with both species.

## 2 | MATERIALS AND METHODS

### 2.1 | Insects

*Tecia solanivora* and *S. tangolias* eggs and adults were obtained from rearing colonies maintained at the National Institute for Agricultural Research (INIAP) in Gutuglahua, Pichincha province, Ecuador, at room temperature of 15 ± 5°C. Both rearing colonies were started and renewed with adults collected from potato stores in the Cotopaxi and Chimborazo provinces of Ecuador at altitudes of 2,700–3,10 masl. The adults were kept in oviposition tubes (diameter 8.5 cm, height 10 cm) that were covered on both sides with organza cloth. Cotton pieces soaked with honey–water (1:4) were fixed in the tube to provide a food source. Eggs were laid on filter paper placed below and upon the oviposition tubes. The filter paper was collected weekly, and hatching larvae were reared on potato tubers (var. Superchola). Corrugated cardboard was provided as pupation site. Pupae were collected from the cardboard, and the emerging adults were placed in oviposition tubes.

### 2.2 | Bioagents

*Dipel 2X®* (WP), Valent Biosciences, Illinois, USA, active ingredient *B. thuringiensis* Berliner subsp. *kurstaki* (64 g/kg) (Btk) was obtained from a local agrochemical supply store. *P. operculella* granulovirus (PhopGV), isolate JLZ9f, was obtained from the powder formulation “Granulovirus” produced at INIAP-UVTT Carchi, San Gabriel, Ecuador. JLZ9f had originally been isolated from *P. operculella* in Cuchitingue, Cotopaxi Province, Ecuador, and is maintained at the Catholic University in Quito, Ecuador. To get a more concentrated viral solution, 100 g of the granulovirus powder was dissolved in 1 L of distilled water. Pieces of filter paper containing *T. solanivora* eggs (obtained from insect rearing) were submerged in the solution for 30 s. Eggs were dried on a paper towel before they were placed on potato tubers.
and reared until the 4th larval instar. The whitish PhopGV-infected larvae were collected after leaving the tubers and stored in the freezer at −18°C. For application in experiments, the infected larvae were macerated using mortar and pestle, and stock solutions were prepared with distilled water using at least 16 larvae. The concentration is expressed in larval equivalents (LE) per litre of distilled water.

2.3 | Inert substances

Kaolin, sand and calcium carbonate were bought in bulk in the building supply store “Trujillo” in Quito. Talcum (baby talco, Johnson & Johnson) was bought at the pharmacy “Fybeca” in Quito. The pH value of the inert substances was determined in saturated solution with a pH Meter (Table 1). All substances were homogenous and powdery and did stick well to the surface of the potato tubers.

2.4 | Bioassays

Bioassays were conducted for testing bioagents, inert substances, their combinations and the impact of humidity on their efficacy. The experiments were established by treating batches of 1.250 g of washed and dried potato tubers (var. Superchola) with each individual treatment. The treated tubers were distributed into six plastic boxes (diameter 11.5 cm, height 6 cm) representing six replicates. An untreated batch and a batch treated with the inert substance only (if combinations with active ingredients were evaluated) served as control treatments. A piece of filter paper containing 50 T. solanivora eggs each was placed on top of the potato tubers in each of the boxes, together with a piece of corrugated cardboard for pupation. Boxes were covered with a lid containing a window (25 cm²) of organza cloth, and each experiment was arranged completely randomized at room temperature of 17 ± 2°C. After 6 weeks, the number of pupae was assessed and potato tubers were carefully cut to ensure that all individuals were found. Each experiment was repeated twice.

The treatments applied in the bioassays were as follows:

**Bioagents:** PhopGV and Btk were dissolved in distilled water at concentrations of 8, 4, 2, 1, 0.5, 0.025, 0.125 and 0.06 LE/L or 60, 30, 15 and 7.5 g/L, respectively. The potato tubers were submerged and allowed to dry.

**Inert substances:** Potato tubers were filled in plastic bags, and the inert substances were added at a rate of 5 g/kg. Bags were shaken until tubers were covered uniformly.

### TABLE 1 Inert substances evaluated for the control of Tecia solanivora and Symmetrischema tangolias larvae

| Substance        | Main component     | pH²   |
|------------------|--------------------|-------|
| Kaolin           | Al₂Si₂O₅(OH)₄      | 6.7   |
| Sand (<0.1 mm)   | SiO₂               | 7.0   |
| Calcium carbonate| CaCO₃              | 9.2   |
| Talcum           | Mg₃Si₂O₅(OH)₂      | 7.5   |

²Saturated solution in distilled water.

**Impact of humidity:** Calcium carbonate was applied to the potato tubers as described above. Two different levels of humidity were obtained using lids with and without window for the treated tubers as well as for the untreated control. The relative humidity inside the boxes was recorded with one electronic data logger per treatment.

**Inert substances combined with bioagents:** Btk + talcum was tested at rates of 60, 30, 15 and 7.5 g Btk/kg talcum, and PhopGV-kaolin was tested at rates of 25, 5 and 1 LE/kg kaolin. Solutions of the bioagents were prepared, mixed with the inert substance and allowed to dry before they were ground with mortar and pestle. They were stored at 16 ± 2°C for up to 2 weeks until they were applied to the tubers at a rate of 5 g/kg as described above.

2.5 | Storage experiments

Treatments with the highest efficacy to prevent T. solanivora infestation in bioassays were evaluated under simulated storage conditions. Experiments were conducted in two different storage facilities:

Storage 1 was a shaded greenhouse where a roof protected the potato tubers from rainfall and the mesh hindered the entry of birds and insects; temperatures fluctuated between 8 and 18°C. This reflects a common storage practice of farmers who store their potato bags outdoors under a roof or in a hut open on one side. Storage 2, with an indoor room and a mean temperature of 18 ± 2°C, was probably an even more common storage practice. Potato tubers (var. Superchola) were washed and dried before batches for each treatment and replicate were prepared. The batches were put into plastic bags, powdered with the respective formulation at a rate of 5 g/kg, and were shaken until the potatoes were covered uniformly. Each treatment was filled in a net lace bag and infested with 1- to 2-day-old T. solanivora or S. tangolias adults; the bags were sealed with a rubber band. When the developed larvae had reached the L2–L3 larva stage, the infested potato tubers were filled in tight plastic bags or containers to prevent larvae from escaping; corrugated cardboard was provided for pupation. The experiment was conducted until pupation of the first generation, which took place after 3.5 months in storage 1 and after 2 months in storage 2. The potato tubers were cut in two pieces and classified into four categories according to the infestation intensity on the cross-sectional area: no damage, minimal damage (<5% of the area affected), medium damage (5%–20% of the area affected) and total damage (>20% of the area affected). The fraction of damaged potato tubers (<5% to >20%) was expressed as infestation rate (%). Potato tubers and the cardboard were searched for pupae and dead larvae.

The treatments applied in the storage experiments were as follows:

**Inert substances combined with bioagents:** The powder formulations based on calcium carbonate containing PhopGV and Btk were prepared as described for the bioassays at rates listed in Table 2. Batches of 2 kg of potato were used for each replicate, and the experiment was arranged in a randomized complete block design with five replicates. Over a period of 4 days, each bag was infested with eight females and five males.
Calcium carbonate combined with three different storage conditions: Batches of 14 kg of potato per replicate were powdered with calcium carbonate and put into thin layers, mesh bags, or compact bags, which is the most common storage method used by farmers. Each batch was infested with 15 females and eight males. The calcium carbonate powdered batches were arranged with untreated control batches in a randomized complete bloc design with four replicates separately for each type of storage and moth species. The relative humidity in between untreated potato tubers stored in a thin layer or in a mesh or compact bag was determined at 15°C and 60%–70% ambient humidity using electronic data loggers.

2.6 | Statistical analysis

All experiments were repeated twice. When the impact of the treatments was similar in both experiments according to a two-way analysis of variance at \( p > .05 \) (\( F \) test), the data from the two experiments were pooled. Data were checked for normal distribution of residuals with the Shapiro–Wilk test and for homogeneity of variance with Levene’s test before they were subjected to analysis of variance (ANOVA). If necessary, data were square root transformed. Percentage data were always arcsine transformed. The Tukey test was performed to determine significant differences between treatments at \( p < .05 \). Mortality in treatments was corrected using the formula given by Abbott (1925):

\[
\text{Effective mortality rate} = \frac{\text{dead individuals in the treatment} - \text{dead individuals in the control}}{100 - \text{dead individuals in the control}}
\]

3 | RESULTS

3.1 | Bioassays

3.1.1 | Efficacy of PhopGV and Btk against T. solanivora

PhopGV was effective against T. solanivora with a LC\(_{50}\) of 0.33 LE/L (CI 95% 0.26–0.40) (Figure 1). At the highest rate of 8 LE/L, mortality was 97.1%. The number of dead L4-larvae with signs of viral infection increased with the concentration, and there were no significant differences (\( F = 0.77, df = 8, p = .63 \)) in the sum of dead L4-larvae and surviving individuals across concentrations, which indicates that infected larvae died in the L4 stage. Btk did also increase larval mortality significantly (\( F = 20.39, df = 3, p < .001 \)). At the highest concentration of 100 g/L, mortality reached 82.7% (Figure 2).
3.1.2 Efficacy of inert substances for the control of *T. solanivora* and *S. tangolias*

The inert substances had a protective effect which did impede larval infestation of potato tubers. Very few dead L2–L4 larvae were observed, and infestation rate and intensity on potato tubers was low in all treatments. That means that larvae had already died during the L1; at this stage, larvae cannot be found during the evaluation. Mortality of *S. tangolias* was not significantly different between inert substances \((F = 2.47, df = 3, p = .074)\) and ranged between 84.6% and 98.6% (Figure 3). For *T. solanivora*, the difference between inert substances was significant \((F = 3.46, df = 3, p = .028)\), and the mortality of 95.4% caused by calcium carbonate was significantly higher than the mortality of 76.2% caused by talcum.

3.1.3 Efficacy of bioinsecticides combined with inert substances for the control of *T. solanivora* and *S. tangolias*

As the efficacy of the inert substances on *T. solanivora* larvae was already high in most cases, differences between the various concentrations of the active ingredients Btk and PhopGV were small. Talcum alone led to a mortality of 61.5% and Btk at rates of 30 and 60 g/kg of talcum increased the mortality of *T. solanivora* larvae significantly to 87.4% and 88.1%, respectively \((F = 5.20, df = 4, p = .013)\) (Figure 4a). In the kaolin-PhopGV treatment, kaolin alone caused in the first experiment 18.0% mortality of *T. solanivora* larvae. PhopGV increased the mortality significantly to 94.6% and 99.1% at the rates of five and 25 infected larvae/kg of kaolin \((F = 46.27, df = 3, p < .001)\) (Figure 4b). In the second experiment, kaolin alone caused 97.8% mortality, and no additional effect of PhopGV could be observed \((F = 2.54, df = 3, p = .0856)\). Owing to the low efficacy of kaolin in the first experiment with PhopGV, the number of larvae that died after reaching the 4th instar due to viral infection was higher than in the second experiment, as was the infestation intensity of the potato tubers.

3.1.4 Impact of the air circulation on the efficacy of calcium carbonate for the control of *T. solanivora*

Air circulation kept relative humidity at 70%–85% meanwhile without air circulation, relative humidity increased to 100% within 1–2 days. Calcium carbonate caused 55.4% mortality without air circulation; air circulation did increase mortality significantly to 96.2% \((F = 45.27, df = 1, p < .001)\) (Figure 5).

3.2 Storage experiments

3.2.1 Efficacy of bioinsecticides combined with inert substances for the control of *T. solanivora* and *S. tangolias*

Owing to lower temperatures at storage 1, development time was about two times longer than at storage 2 and the experiment lasted for almost 4 months. At the same time, the reproduction of *T. solanivora* and *S. tangolias* was 1.5 and four times higher at storage 1, with 534 vs. 358 and 444 vs. 119 individuals developed in the untreated control. The efficacy of the treatments was similar, and the two experiments were evaluated jointly. All treatments increased the mortality of *T. solanivora* and *S. tangolias*, and significantly reduced infestation rate and infestation intensity of potato tubers compared with the untreated control (Table 3, Figure 6). Calcium carbonate alone caused 97% mortality of *T. solanivora* and reduced the infestation rate of...
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potato tubers by 91%, whereby the category with infestation intensity >20% was reduced from 72.6% in the untreated control to 29.5% of all damaged tubers. Adding either Btk or PhopGV did not improve efficacy of calcium carbonate; however, a significant difference was observed between the mortality rate in the Btk (95.0%) and PhopGV (99.8%) treatment (\(F = 5.01, df = 3, p = .0053\)). There was no significant difference in the infestation intensity between the treatments (\(F = 1.83, df = 3, p = .1585\)). In S. tangolias, calcium carbonate alone caused mortality of 84.5% and reduced the infestation rate by 56.8%, whereby the category with infestation intensity >20% was reduced from 61.7% in the untreated control to 29.0% of all damaged tubers. Calcium carbonate in combination with Btk was significantly more effective increasing the mortality of S. tangolias to 96.5% (\(F = 6.46, df = 3, p = .0013\)) as well as reducing tuber infestation rate by 83.4% (\(F = 15.06, df = 3, p < .0001\)). The addition of PhopGV did not increase efficacy of calcium carbonate.

3.2.2 | Efficacy of calcium carbonate under three different storage conditions for the control of T. solanivora and S. tangolias

The storage conditions did influence the relative humidity. In the thin layer storage, relative humidity was 60–80%, in the mesh bag 97–100%, and in the compact bag 100%.

The effect of calcium carbonate on pest incidence was significant at both storage sites 1 and 2 for both species (Table 4). The storage conditions had a significant impact on T. solanivora incidence at storage 1 and on S. tangolias incidence at storage 2; in both cases, the

TABLE 3 Efficacy of calcium carbonate (cc) applied alone or in mixture with Btk and/or PhopGV on stored potato tubers to prevent Tecia solanivora or Symmetrischema tangolias infestation

| Species          | Treatments | Mortality (%) | Reduction of the infestation rate (%) |
|------------------|------------|---------------|---------------------------------------|
| T. solanivora    | cc         | 97.1 (±0.96)abc,+ | 91.0 (±2.14)abc,+                     |
|                  | cc+Btk     | 95.0 (±1.76)a+  | 83.6 (±2.76)a+                         |
|                  | cc+PhopGV  | 99.8 (±0.09)a+  | 91.0 (±3.03)a+                         |
|                  | cc+Btk+PhopGV | 97.9 (±0.58)abc,+ | 89.7 (±2.35)a+                         |
| S. tangolias     | cc         | 84.5 (±3.18)c+  | 56.8 (±3.15)c+                         |
|                  | cc+Btk     | 96.5 (±1.33)a+  | 83.4 (±4.70)a+                         |
|                  | cc+PhopGV  | 83.7 (±3.74)bc+ | 48.9 (±2.47)bc+                        |
|                  | cc+Btk+PhopGV | 94.0 (±2.10)abc,+ | 82.8 (±5.00)abc,+                     |

Values are means of two experiments. Means with the same letter within one column and species are not significantly different at \(p \leq .05\) according to the Tukey test. Values in parenthesis are standard errors of the mean.

*Mortality and reduction of the infestation rate were significantly different compared with the untreated control at \(p \leq .05\) according to the t test.

FIGURE 5 Corrected mortality (Abbott, 1925) of neonate Tecia solanivora larvae feeding on potato tubers powdered with calcium carbonate that were stored in boxes with and without air circulation. Values are the means of two experiments. Vertical bars indicate the standard error. Means with the same letter are not significantly different (ANOVA, \(p < .0001\))

FIGURE 6 Tecia solanivora (a) and Symmetrischema tangolias (b) infestation intensity on potato tubers treated with calcium carbonate (cc) alone or in mixture with Btk and/or PhopGV in a storage experiment. The experiment was repeated twice; values are the means of the two experiments.

3.2.2 | Efficacy of calcium carbonate under three different storage conditions for the control of T. solanivora and S. tangolias

The storage conditions did influence the relative humidity. In the thin layer storage, relative humidity was 60–80%, in the mesh bag 97–100%, and in the compact bag 100%.

The effect of calcium carbonate on pest incidence was significant at both storage sites 1 and 2 for both species (Table 4). The storage conditions had a significant impact on T. solanivora incidence at storage 1 and on S. tangolias incidence at storage 2; in both cases, the
effect of interaction was significant. For *T. solanivora* at storage 2, the efficacy of calcium carbonate was very high under all storage conditions; however, for *S. tangolias* at storage 1, the efficacy of calcium carbonate was rather low under all storage conditions. In these cases, the way of storage had no significant impact nor were interactions significant.

Calcium carbonate was highly effective at controlling *T. solanivora* and *S. tangolias* under all kinds of storage conditions at storage 2, and pest incidence and infestation rate were reduced in all cases significantly compared with the untreated control (Figure 7, Table 5). At storage 1, the variation in infestation between replicates was high, especially in the case of *T. solanivora*, due to splash water affecting tubers in the first two rows of the experiment. Among species, the efficacy of calcium carbonate was higher for *T. solanivora* than for *S. tangolias*. Furthermore, storage conditions affected the efficacy of treatments. Calcium carbonate was more efficient when tubers were stored in thin layers, which reduced the number of *T. solanivora* individuals by 91.4% and 96.9% and of *S. tangolias* by 68.1% and 89.8% in storage 1 and storage 2, respectively. Likewise, the number of infested potato tubers was reduced by 73.1% and 71.9% for *T. solanivora* and by 55.4% and 59.0% for *S. tangolias* at storage in thin layers at storage 1 and storage 2; also, the infestation intensity decreased. Potato tubers used for trials at storage 2 had a low initial infestation that was recognized only after the experiment had been started. Last-instar larvae appearing within 3 weeks after the experiment was set up were removed, but tubers had been infested already. Therefore, the infestation rate was higher

| Location  | Species     | Factor                  | df | F-value | p     |
|-----------|-------------|-------------------------|----|---------|-------|
| Storage 1 | *T. solanivora* | Storage conditions     | 2  | 6.02    | .0100 |
|           |             | Cc powder vs. Control   | 1  | 71.63   | <.0001|
|           |             | Interactions            | 2  | 4.00    | .0364 |
|           | *S. tangolias* | Storage conditions     | 2  | 2.41    | .1179 |
|           |             | Cc powder vs. Control   | 1  | 13.45   | .0018 |
|           |             | Interactions            | 2  | 2.53    | .1073 |
| Storage 2 | *T. solanivora* | Storage conditions     | 2  | 0.87    | .4344 |
|           |             | Cc powder vs. Control   | 1  | 186.02  | <.0001|
|           |             | Interactions            | 2  | 0.02    | .9784 |
|           | *S. tangolias* | Storage conditions     | 2  | 6.12    | .0094 |
|           |             | Cc powder vs. Control   | 1  | 130.34  | <.0001|
|           |             | Interactions            | 2  | 3.76    | .0431 |

*df*, degrees of freedom; *p*, significance level.

**TABLE 4** Two-way ANOVA of the impact of “storage conditions” and “cc powder vs. control” and their interactions on the incidence of *Tecia solanivora* and *Symmetriscchema tangolias* in stored potato tubers at two locations

**FIGURE 7** *Tecia solanivora* and *Symmetriscchema tangolias* infestation intensity in two storage experiments on potato tubers that were treated with calcium carbonate (cc) or kept untreated (control) and stored in thin layers, mesh bags or compact bags
TABLE 5  
**Tecia solanivora** and **Symmetrischema tangolias** incidence and infestation rate on potato tubers stored in thin layers, in mesh bags, or in compact bags at two storage locations; tubers were powdered with calcium carbonate (cc) or kept untreated (control)

| Location | Species     | Storage conditions | Control (SE) | cc (SE) | Efficacy (%) | Infestation rate (%) | Control (SE) | cc (SE) | Efficacy (%) |
|----------|-------------|--------------------|--------------|---------|--------------|----------------------|--------------|---------|--------------|
| Storage 1| T. solanivora| Thin layer         | 1505 (27.3)  | 130 (86.5) | 91.4<sup>a</sup> | 65.2 (1.73)          | 17.5 (7.94)  | 73.1<sup>a</sup> |
|          |             | Mesh bag           | 1833 (193.6) | 654 (251.9) | 64.3<sup>a</sup> | 74.4 (3.14)          | 46.6 (10.90) | 37.3<sup>a</sup> |
|          |             | Compact bag        | 1876 (76.5)  | 241 (44.5)  | 87.1<sup>a</sup> | 78.1 (2.80)          | 30.4 (2.23)  | 61.1<sup>a</sup> |
|          | S. tangolias | Thin layer         | 948 (59.8)   | 303 (54.5)  | 68.1<sup>a</sup> | 77.7 (2.74)          | 34.6 (3.99)  | 55.4<sup>a</sup> |
|          |             | Mesh bag           | 934 (147.0)  | 778 (138.9) | 16.7          | 82.3 (2.23)          | 68.4 (6.72)  | 16.8<sup>a</sup> |
|          |             | Compact bag        | 956 (99.5)   | 715 (153.5) | 25.3          | 86.9 (2.84)          | 63.1 (7.99)  | 27.4<sup>a</sup> |
| Storage 2| T. solanivora| Thin layer         | 369 (46.5)   | 11 (4.5)    | 96.9<sup>a</sup> | 60.3 (4.69)          | 16.9 (2.08)  | 71.9<sup>a</sup> |
|          |             | Mesh bag           | 534 (51.3)   | 17 (4.9)    | 96.9<sup>a</sup> | 67.2 (2.91)          | 19.2 (0.77)  | 71.4<sup>a</sup> |
|          |             | Compact bag        | 474 (72.6)   | 14 (3.6)    | 97.1<sup>a</sup> | 72.6 (6.24)          | 15.4 (2.47)  | 78.8<sup>a</sup> |
|          | S. tangolias | Thin layer         | 664 (88.6)   | 68 (17.6)   | 89.8<sup>a</sup> | 69.9 (1.83)          | 28.7 (1.53)  | 59.0<sup>a</sup> |
|          |             | Mesh bag           | 752 (43.2)   | 145 (50.3)  | 80.7<sup>a</sup> | 78.9 (2.98)          | 32.1 (2.34)  | 59.3<sup>a</sup> |
|          |             | Compact bag        | 730 (49.4)   | 311 (57.6)  | 57.4<sup>a</sup> | 81.1 (0.81)          | 39.5 (2.70)  | 51.3<sup>a</sup> |

<sup>a</sup>Treatments with and without application of calcium carbonate are significantly different at p ≤ .05 according to the t test.

than expected in the treatments with high mortality. The category with infestation intensity >20% was reduced compared to the untreated control from 45.8% to 24.4% and from 31.9% to 13.4% for *T. solanivora*, and from 46.2% to 30.9% and from 29.8% to 13.0% for *S. tangolias* at storage 1 and storage 2, respectively, when potato tubers were stored in thin layers. Among untreated potato tubers, the percentage of infested tubers was positively related to humidity. For both species and storages, infestation of tubers was lowest in thin layer, medium in mesh bags and highest in compact potato bags.

4  | **DISCUSSION**

4.1  | **Efficacy of PhopGV and Btk against *T. solanivora* in bioassays**

*Phthorimaea operculella* granulovirus (PhopGV), isolate JLZ9f, and *Bacillus thuringiensis* subsp. *kurstaki* (Btk), formulated in the product Dipel 2X<sup>®</sup> (WP), caused disease in *T. solanivora* and finally killed larvae. The virulence of the PhopGV, isolate JLZ9f, was comparable to the virulence of a locally isolated granulovirus in Venezuela from *T. solanivora* that caused 45%–51% mortality in *T. solanivora* larvae at a rate of 1 LE/L (Niño & Notz, 2000). Activity of Btk on *T. solanivora* was about 8 and 19 times lower than reported by Mamani (2008) for *S. tangolias* (*LC<sub>50</sub> = 3.1 g/L*) and *P. operculella* (*LC<sub>50</sub> = 1.3 g/L*) using the same product. However, these liquid applications of PhopGV and Btk used in bioassays are not a reasonable and practical option to protect stored potatoes from potato tuber moth infestation. After application, tubers need to dry before placing them in stores. As PhopGV and Btk are quickly inactivated by sunlight, an application and subsequent drying outdoors before storage can already reduce its long-term efficacy. Furthermore, after a liquid application the distribution of granules on tubers is inhomogeneous requiring a higher concentration of PhopGV (>8–9 LE/L) to obtain larvae mortality of 95% and even a high rate of Btk at 100 g/L only caused larvae mortality of 82.7%. It needs also to be considered that PhopGV-infected *T. solanivora* larvae mostly first die during their last larval instars when a concentration of 8 LE/L is used, which means that tuber damage cannot be completely prevented. A formulation with inert substances would ease application and increase the efficacy of the treatment.

4.2  | **Efficacy of inert substances against *T. solanivora* and *S. tangolias* in bioassays**

Powder applications of inert substances to the surface of potato tubers have a protective effect against young *T. solanivora* and *S. tangolias* larvae which try to enter the potato tuber. Our study confirmed that the inert substances calcium carbonate, kaolin, talcum and sand are highly effective at controlling both tuber moth species. We furthermore showed that relative humidity caused by the respiration of potato tubers and lack of air circulation decreases the activity of calcium carbonate significantly. Inert substances are supposed to affect neonate larvae for their physical abrasive activity and desiccation, as the dust damages the waxy layer from the cuticle of the larvae (Golob, 1997; Hill, 2002, p. 416; Kroschel, 1995). The reduced mortality observed at high humidity levels might be caused by a compensation of the desiccating effect of the inert substances.

Differences in humidity might be an important factor for the variation in efficacy reported by different authors. In our study, calcium carbonate, kaolin, talcum and sand controlled *S. tangolias* by 98.7%, 97.3%, 90% and 84.6%, respectively, whereas Mamani et al. (2011) observed lower efficacies of only 15.6%, 35.9%, 42.5% and 10% for the same four inert substances. Mamani et al. (2011) also evaluated the efficacy of these inert substances against *P. operculella*, which co-occurs frequently with *S. tangolias*, and observed lower efficiencies of
9–36%. In contrast, Kroschel and Koch (1996) reported a 94.6% mortality for first-instar *P. operculella* larvae on potato tubers powdered with quartz-rich sand. Other factors for the variation in efficacy might be different qualities of the inert substances used or different application techniques that might lead to variation in tuber coverage.

### 4.3 Efficacy of PhopGV and Btk formulations on *T. solanivora* and *S. tangolias* in bioassays

The dose–response bioassays with PhopGV and Btk formulations had been conducted to define the appropriate application rate. As the efficacy of the inert substance was high in most cases, the explanatory power on the dose efficacy was limited. For PhopGV, a dose ≥5 LE/kg kaolin caused >95% larval mortality on *T. solanivora*; this is similar to mortality of 88.4%, 98.2% and 99.1% for 5, 10 and 15 LE/kg of calcium carbonate reported by Carpio et al. (2013). Sotelo et al. (2004) observed 80–100% efficacy to control *T. solanivora* at a PhopGV dose of 20–40 LE/kg of kaolin in bioassays. PhopGV at a dose of 20 LE/kg was used to test the efficacy of calcium carbonate with and without PhopGV to control *T. solanivora* under storage conditions.

The *Btk* formulation reached an acceptable level of *T. solanivora* control of 87.4% at concentrations ≥30 g *Btk*/kg talcum in our study. For *S. tangolias*, Mamani (2008) had observed 94% mortality at the rate of 15 g *Btk*/kg. Preliminary experiments, however, had also shown that even rates of 100 g *Btk*/kg of inert substances do not provide reliable control of *T. solanivora* when the activity of the inert substance is low. Therefore, *Btk* was not considered an economically viable option for the control of *T. solanivora*, compared with the use of PhopGV, which in Ecuador has a production cost of US$2.68/kg of formulated product and provides reliable control of >90% (Suquillo et al., 2011b). However, as *Btk* might increase the efficacy of inert substances against *S. tangolias*, a formulation with *Btk* at a dose of 15 g/kg was selected for the evaluation in the storage experiment.

### 4.4 Efficacy of bioinsecticides combined with inert substances for the control of *T. solanivora* and *S. tangolias* under storage conditions

For the evaluation of bioinsecticides in storage, calcium carbonate was selected as inert substance for its high efficacy and its low variability, especially compared to talcum and sand, in preliminary experiments. Further advantages were the low quantity of water required to obtain homogenous mixtures with the bioagents, which shortened the time for drying, and the local availability. It is known that an alkaline pH value might impact the efficacy of PhopGV and *Btk*. However, in the storage experiments most larvae found were infected with PhopGV. In case of *Btk*, significant effects on *S. tangolias* mortality proved its high activity. However, it cannot be excluded that the activity of the bioagents might have been even higher in combination with a pH neutral inert substance. However, the results from this study indicate that it is unnecessary to add PhopGV to calcium carbonate as the application of this inert substance alone is highly active to reduce infestation by *T. solanivora* (97.1%). It is comparable to the efficacy of formulations with PhopGV evaluated in other studies. Gómez-Bonilla, López-Ferber, Caballero, Murillo, and Muñoz (2013) reported a 3.5- to sixfold lower infestation with *T. solanivora* and *P. operculella* after application of a PhopGV-talcum formulation. In Ecuador and Colombia, semi-industrially produced PhopGV formulations were evaluated against *T. solanivora* in potato stores and reduced infestation by 90–100% (Sotelo et al., 2004; Suquillo et al., 2011b).

Activity of calcium carbonate against *S. tangolias* was lower than for *T. solanivora*, and the addition of *Btk* did improve efficacy. Mamani (2008) reported a 4–5 times lower *S. tangolias* infestation of potato tubers protected with a 15 g *Btk*/kg of talcum formulation in Peruvian storage facilities after 6 months of storage; he also reported high efficacy against *P. operculella*. In the present study, the 15 g *Btk*/kg of calcium carbonate formulation reduced the *S. tangolias* infestation by 20 times after 4 months of storage. The higher tolerance of *S. tangolias* towards calcium carbonate in the storage experiment might be caused by the morphology of neonate larvae. *T. solanivora* larvae have a longer, transparent body, whereas *S. tangolias* larvae are more compact and have a dark coloration. Therefore, *S. tangolias* larvae are likely less susceptible to wounding and dehydration. A formulation of 15 g *Btk*/kg of calcium carbonate might protect potato tubers effectively against the three potato tuber moth species. In regions where *T. solanivora* is the only important storage pest, calcium carbonate alone would be sufficient.

### 4.5 Efficacy of calcium carbonate under three different storage conditions for the control of *T. solanivora* and *S. tangolias*

Efficacy of calcium carbonate against *T. solanivora* and *S. tangolias* was clearly influenced by the relative humidity under the different storage conditions and sites. Humidity, and therefore infestation rate and intensity, was lowest in thin layer storage inside a closed room (site 2). Thin layer storage did not allow humidity to accumulate, and storage inside a closed room protected potato tubers from splash water during heavy rainfall, which did reduce efficacy in some of the batches stored under a roof (site 1) dramatically. Considering the problems with splash water at storage site 1, and with initial tuber infestation before the start of the experiment at storage site 2, efficacy against *T. solanivora* under ideal storage conditions (dry, no initial infestation) would be expected to be similar to the efficacy observed in dry batches at site 1, with up to 98% reduction in individuals and up to 88% reduction in the infestation rate. Against *S. tangolias*, efficacy of calcium carbonate alone was more homogeneous and with maximum 89.8% reduction of individuals and 59% reduction of the infestation rate considerably lower compared with *T. solanivora*. Therefore, calcium carbonate combined with dry storage can be a suitable option for farmers mainly in regions where *T. solanivora* is the predominant pest species. Thin layer storage is preferable for its higher efficacy against *S. tangolias* and at higher humidity levels, but storage in bags is also suitable if the storage is dry and *T. solanivora* is the main pest species.
Storage under dry conditions is also important if a PhopGV formulation was applied, as T. solanivora larvae infected with PhopGV do not die immediately but just before pupation when the damage to the potato tubers is already done. This damage caused by the first generation would be comparable to the damage in the untreated control as the experiment was stopped after pupation of the first generation. Therefore, adding PhopGV would have a protective effect only against the next generation of T. solanivora, which would develop after about 3 months. A treatment with calcium carbonate alone would have several advantages over a formulation with Btk or PhopGV: Calcium carbonate is cheap, with a price of US$0.20/kg, is easily available, and requires no further formulation. In contrast to formulations containing active ingredients, it does not expire and is not affected by sunlight.

5 | CONCLUSION

Bioassays as well as storage experiments did indicate a clear impact of humidity on the efficacy of inert substances and did confirm the high efficacy of calcium carbonate to control T. solanivora under dry storage conditions. This finding is important as this technique is cheap and readily available to farmers and could be used widely. We recommend evaluating calcium carbonate applications in farmers’ storages in regions where T. solanivora is the prevalent pest species. Therefore, potatoes need to be stored in a way that ensures sufficient air circulation to keep relative humidity at a level not affecting the mode of action of inert substances. Storage in shelf structures or in mesh bags is appropriate for this purpose. For regions with co-occurrence of T. solanivora and S. tangolias in stored potatoes, a formulation of 15 g Btk/kg of calcium carbonate is recommended to be evaluated under farmers’ storage conditions.

ACKNOWLEDGEMENTS

The authors are grateful for the financial support supplied by the German Academic Exchange Service (DAAD).

AUTHOR CONTRIBUTION

Study design, data collection and analysis as well as drafting of the article was done by BS. Critical revision of the study and of the article was done by JK.

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How to cite this article: Schaub B, Kroschel J. Developing a biocontrol strategy to protect stored potato tubers from infestation with potato tuber moth species in the Andean region. J Appl Entomol. 2018;142:78–88. https://doi.org/10.1111/jen.12426