

Trade-off and adaptive cost in a multiple-resistant strain of the invasive potato tuber moth *Tecia solanivora*

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Abstract

BACKGROUND: Resistance to pesticides is an evolutionary process that entails, in most cases, substantial consequences to the biology of the resistant populations. In this study we focus on the life history traits of the potato tuber moth *Tecia solanivora*, an invasive and voracious pest for which resistance to pyrethroid insecticides was recently reported.

Marginally resistant and multiple-resistant populations were selected from eight sampled localities in Colombia; the use of a fully susceptible population was not possible since none was recognized in the laboratory or field. The multiple-resistant Siachoque population exhibited a 42-fold resistance to the carbamate insecticide carbofuran, and low levels of resistance to chlorpyrifos, a trend observed in six of the eight tested populations. This population also exhibits 24-fold resistance to permethrin. The marginally resistant population of Gualmatán showed 4-fold resistance to chlorpyrifos.

RESULTS: The multiple-resistant population exhibited a 3.8-day shorter developmental time than the susceptible population, but with higher larval mortality. The peak of egg-laying was delayed in the resistant population in 9 days and the population growth rate was lower than that of the susceptible population.

CONCLUSION: We hypothesize that the short developmental time of the multiple-resistant population may be an adaptation to minimize exposure to insecticides, which are applied to the soil. This adaptation is likely to require the surviving adults to compensate for the smaller nutrient amounts accumulated by the larvae in investing part of its adult life in securing the necessary resources for late-life egg production.

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Keywords: toxicology; carbofuran; chlorpyrifos; fitness; resource allocation; *Scrobipalopsis solanivora*

1 INTRODUCTION

Resistance to pesticides has been documented for over a century.¹ Several studies have been carried out detailing its mechanisms and consequences in several hundreds of arthropod species,^{2,3} including the molecular basis for this remarkable evolutionary process.^{4–6} The evolution of insecticide resistance in a population involves mutations that, while furnishing the insects with the ability to thrive in highly managed agroecosystems, can also impose severe deleterious effects that compromise the fitness of the resistant individuals in the absence of the selection agent, the insecticide.⁷

Through the known mechanisms of insecticide resistance (e.g. metabolic detoxification through up-regulation, change in coding sequence, down-regulation), physiological and biochemical changes are expected in resistant populations.^{8–10} Life history traits (e.g. development, reproduction, longevity) can also be affected as a consequence of physiological constraints and trade-offs allowing survival at the expense of other traits.⁷

Arthropods exhibit a myriad of life history strategies due to the high diversity of niches and habitats they occupy.¹¹ For instance,

most lepidopterans spend the larval stages accumulating nutrients that they will subsequently use for egg production.^{12,13} In fact, many moths carry partially developed eggs by the time of adult emergence.¹² Thus, when changes in the environment (i.e. biotic or abiotic factors) force the populations to change their life history strategy, this implies a physiological cost.⁹ The cost of insecticide resistance, for instance, is thought to be associated with the reallocation of resources for maintenance of defensive mechanisms that

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the resistant populations have evolved, which seems particularly important when enhanced insecticide detoxification is the prevailing resistance mechanism.⁷

Detrimental effects on fitness are commonly associated with resistance to pesticides.^{7,14} Conversely, several studies carried out in a variety of insect taxa demonstrate that insecticide resistance does not always implies fitness costs.^{15–19} In fact, the cost of insecticide resistance may be not apparent under the tested conditions (i.e. environmental variables), may not be statistically significant, or simply may not exist depending on the prevailing resistance mechanism, among other causes.^{7,9}

A recent concern with insecticide resistance and associated fitness costs emerged with the invasive potato tuber moth *T. solanivora* (Lepidoptera: Gelechiidae), a species native of Guatemala in Central America.²⁰ This species has been recorded attacking only potato tubers (*Solanum tuberosum* L.), both in the field and in storage facilities. Its distribution has expanded latitudinally and altitudinally since 1970.^{21,22} Nowadays this tuber moth is considered widely distributed in the Neotropical region,^{23,24} where the reported economic losses have been as high as 100%.²³ The species started to spread overseas (by means of seed distribution) in 1999,^{21,25} and it is expected to reach mainland Africa and establish in Europe in the years to come.^{26,27} Insecticide use against this species, especially in invaded areas, led to emerging problems of insecticide resistance and increased risks of insecticide control failure.²⁰ However, if insecticide resistance is associated with fitness disadvantage, suitable resistance management tactics may delay or prevent the onset of the phenomenon.^{7,9,10}

The aim of this study was first to test if populations of the potato tuber moth *T. solanivora*²⁶ in the Colombian territory bearing a previously known (altered target-site) mutation for resistance to a pyrethroid insecticide²⁸ were also resistant to other insecticides commonly used in potato crops. Subsequently, after identifying two key populations – one nearly susceptible to all tested pesticides (or only marginally resistant, if no susceptible was available), and one resistant to organophosphates and pyrethroids – we recorded and compared their life history traits under pesticide-free conditions to assess if life history trade-off and fitness cost are expressed.

2 MATERIALS AND METHODS

2.1 Populations of *Tecia solanivora*

Infested potato tubers (30–60 kg per site) were collected in several localities in the Nariño department (Colombia) from December 2012 to May 2013 (Table 1). About 400 adults were used to establish stock cultures of every locality. For further information about population maintenance, see Bacca *et al.*²⁸ An additional population from Siachoque (Boyacá, Colombia), already cultured by the Colombian Corporation for Agricultural Research (Corpoica, Bogotá, Colombia), was included because of its known resistance to pyrethroid insecticides.²⁸ All experiments were conducted under laboratory conditions (14 ± 2 °C and $70 \pm 5\%$ RH) at the University of Nariño (Pasto, Colombia), conditions representative of the potato cultivation areas of Colombia.

2.2 Concentration-mortality bioassays

The concentration-mortality bioassays to determine the relative toxicity and resistance in the potato tuber moth populations were performed with the insecticides chlorpyrifos (Lorsban 4 EC, Dow AgroSciences, Bogotá, Colombia) and carbofuran (Furadan 3 SC,

Table 1. Localities of the origin of *Tecia solanivora* populations used in the study

Locality	Height	Coordinates	
Guaitarilla	2635	1° 6' 35.43''N	77° 33' 24.64''W
Gualmatán	2944	0° 55' 5.9''N	77° 34' 32.6''W
Iles	2985	0° 59' 3.23''N	77° 30' 27.7''W
Ipiales	2969	0° 50' 29.7''N	77° 40' 16.6''W
Ospina	2755	1° 3' 15.85''N	77° 34' 49.9''W
Pasto	2800	1° 8' 54''N	77° 18' 41.5''W
Potosí	2660	0° 49' 58.11''N	77° 33' 35.6''W
Siachoque ^a	2760	5° 30' 47''N	73° 14' 39''W

^a All localities lie in Nariño department except Siachoque, which belongs to Boyacá department.

FMC Latinoamérica, Bogotá, Colombia), both used at the following concentrations: 0.01, 0.1, 1, 10, 100, 1000 and 10 000 ppm of active ingredient (a.i.). These insecticides were used because they are commonly employed in potato crops of the Neotropical region.^{21,22,29,30} Chlorpyrifos is a non-systemic broad-spectrum organophosphate with substantial ecological effects because of its toxicity specially to aquatic organisms and is also known for its persistence in sediments.^{31,32} Carbofuran is a systemic broad-spectrum carbamate commonly applied to the soil, and regarded as highly toxic for both terrestrial and aquatic animals.³¹ Although carbofuran is not approved for use against the potato tuber moth, this compound is recurrently applied for the control of the Andean potato weevil (*Premnotrypes vorax* Hustache, 1933) in areas where *T. solanivora* also occurs, allowing for potential inadvertent selection for resistance. Carbofuran activity in this scenario will be mainly by contact with egg-laying adults, although eggs and early first instar larvae are also potentially exposed resembling the exposure of the Andean potato weevil.²²

The experimental units encompassed ten adult moths (5–7 days old, sex ratio 1:1) enclosed in 370 mL plastic containers with an air-dried potato tuber (c. 80 g) previously submerged in the insecticide solution, which was prepared in distilled water containing 0.5% of polysorbate 80 (Tween 80, Sigma–Aldrich, Bogotá, Colombia) as emulsifier. The adults are exposed to the insecticide-contaminated tubers mainly during egg-laying. A cotton ball soaked with 10% honey-water solution was provided as food source for the adult insects. Mortality was assessed after 48 h; insects were scored as dead if no movement was noticed after repeated prodding with a soft brush. Every experimental unit was replicated 10 times for every insecticide, concentration and population. Distilled water containing 0.5% polysorbate 80 was used as control treatment.

2.3 Life history traits

2.3.1 Criteria for population selection

The populations of *T. solanivora* from Gualmatán, Nariño (susceptible) and Siachoque, Boyacá (resistant) were chosen for analysis of life history traits. The former population did not exhibit resistance to carbofuran and exhibited only marginal resistance to chlorpyrifos (no fully susceptible population was observed), while the latter exhibited the highest resistance to carbofuran and to the pyrethroid insecticide permethrin according to Bacca *et al.*²⁸ Thus, Siachoque exhibits multiple resistance and therefore is more likely to exhibit associated fitness cost, if it exists, even when compared

with a marginally chlorpyrifos-resistant population (resembling its own resistance to this particular insecticide).

2.3.2 Experimental procedure

Two hundred initial experimental units were established for each population. Every experimental unit had its bottom covered with tissue paper and contained one potato tuber (c. 80 g) as well as five eggs of the potato tuber moth. Each tuber was pierced several times with a sterilized pin to facilitate the penetration of the newly hatched larvae. This was done to allow easier larvae penetration, reducing the natural mortality that otherwise would take place, as determined in preliminary observations.

During the hatching period, all experimental units were inspected daily. Once the larvae infested the tubers, destructive sampling was carried out every four days in ten randomly selected experimental units of every population; this time interval was selected based on preliminary observations. Such tubers were sectioned to record larvae survival and developmental stage; the inspected tubers were discarded afterwards. Mortality of larvae was indirectly assessed by counting the final number of pupae, which were recorded non-destructively as the insects leave the tuber to produce the pupae. The monitoring of individual larvae was not possible due to the destructive sampling performed.

A subset of 200 individuals of each population reaching pupal stage was randomly selected and housed in couples (1♂:1♀) in 1 L plastic containers; the pupae were sexed according to genital opening placement.³³ Females of the potato tuber moth achieve maximum fecundity after a single mating.^{23,34} Upon reaching adulthood, the insects were provided with a cotton ball soaked in 10% honey–water solution as food source and black crêpe paper as egg-laying substrate. Fecundity and mortality were daily recorded.

2.4 Statistical analysis

The concentration-mortality results were subjected to Probit analyses³⁵ (PROC PROBIT; SAS, SAS Institute, Cary, NC, USA). Insect

mortality from the insecticide treatments was corrected for the natural mortality observed in the control.³⁶ Resistance ratios (RRs) and their respective 95% confidence intervals were calculated at LC₅₀ using the most susceptible population as reference for every insecticide following Robertson *et al.*³⁷; the population was recognized as resistant if its 95% CI for the RR did not incorporate the value 1.³⁷

Life history and reproductive traits were analyzed by means of generalized linear models (GLMs) in R.³⁸ Temporal distribution of egg production was subjected to non-linear regression using the curve-fitting procedure of TableCurve 2D (Systat, San Jose, CA, USA); model selection was based on parsimony, high *F* values and a steep increase in *R*² with model complexity. Survival analysis during the adult stage for females and males of both populations was performed using a log rank test by means of the survival package in R.³⁹ All analyses were performed using data of individuals as experimental units. Fertility life tables were calculated for the both susceptible and resistant populations using SAS (SAS Institute), and following the procedures described by Maia *et al.*,⁴⁰ which allow for confidence intervals and *t*-test calculation.

3 RESULTS

3.1 Relative toxicity of chlorpyrifos and carbofuran

The natural mortality of the potato tuber moth observed in control treatments of the concentration-mortality bioassays remained always lower than 10%, allowing the correction of the observed mortality in the other treatments. The probit model suitably described the corrected concentration-mortality results exhibiting low χ^2 values (≤ 8.02) and high *P* values (≥ 0.05) in the goodness-of-fit tests, allowing the reliable estimation of the desired toxicological endpoints (i.e. LC₅₀ values and derived RR with respective 95% CI). Seven out of the eight populations assessed of the potato tuber moth exhibited resistance to carbofuran and six of them also exhibited resistance to chlorpyrifos (Table 2). Nonetheless, the levels of chlorpyrifos resistance were only marginal (≤ 5.29 -fold), although significant, in contrast with

Table 2. Relative toxicity of carbofuran and chlorpyrifos to populations of the potato tuber moth *Tecia solanivora* studied populations

Insecticide	Population	<i>N</i>	df	Slope ± SEM	LC ₅₀ (95% CI) ppm	LC ₉₅ (95% CI) ppm	χ^2	<i>P</i>	RR (95% CI)
Carbofuran	Gualmatán	500	3	0.89 ± 0.07	5.78 (3.39–10.68)	408.597 (161.979–1391)	5.36	0.15	1 (0.20–4.90)
	Ipiales	400	2	2.99 ± 0.27	28.12 (22.89–34.75)	100 (75.41–145.32)	0.00	1.00	4.86 (1.26–18.71)*
	Guaitarilla	380	2	2.07 ± 0.21	90.39 (70.06–117.45)	562.22 (379.59–972.79)	3.89	0.14	15.61 (3.98–61.28)*
	Iles	350	3	1.56 ± 0.25	169.41 (23.51–543.17)	1922 (598.76–14 886)	8.02	0.05	29.27 (6.64–129.07)*
	Pasto	400	2	2.01 ± 0.27	242.17 (175.76–374.77)	1600 (863.40–4425)	2.60	0.27	41.84 (10.02–174.77)*
	Siachoque	360	2	4.02 ± 0.32	245.020 (211.30–281.87)	629.185 (530.47–776.97)	3.93	0.14	42.33 (4.70–381.34)*
	Potosí	390	3	1.67 ± 0.15	245.05 (187.99–319.55)	2371 (1567–4129)	2.07	0.36	42.34 (9.73–186.50)*
	Ospina	450	2	1.30 ± 0.10	246.48 (178.22–350.41)	4538 (2621–9244)	3.81	0.15	42.59 (10.49–171.04)*
Chlorpyrifos	Potosí	610	4	0.98 ± 0.07	1.90 (1.18–2.96)	89.13 (50.73–177.88)	2.55	0.63	1 (0.53–1.87)
	Ipiales	500	4	1.04 ± 0.08	3.12 (1.99–4.71)	117.55 (67.51–238.04)	5.08	0.27	1.63 (0.90–2.97)
	Ospina	400	3	1.53 ± 0.16	4.74 (3.44–6.47)	56.24 (34.35–113.68)	0.69	0.87	2.48 (1.51–4.11)*
	Iles	300	5	2.04 ± 0.32	5.34 (3.33–8.25)	34.12 (19.71–83.79)	4.27	0.51	2.79 (1.70–4.62)*
	Siachoque	420	5	0.93 ± 0.07	7.34 (4.65–11.26)	415.19 (223.85–915.15)	6.40	0.26	3.84 (1.93–7.65)*
	Pasto	380	3	2.210 ± 0.20	8.12 (6.05–10.64)	45.10 (32.47–68.76)	6.00	0.11	4.26 (2.68–6.77)*
	Gualmatán	600	3	1.03 ± 0.08	8.218 (5.52–11.76)	321.27 (194.48–607.68)	4.28	0.23	4.30 (2.39–7.75)*
	Guaitarilla	400	2	1.95 ± 0.18	10.10 (7.92–12.93)	69.80 (47.39–119.16)	2.83	0.24	5.29 (3.29–8.52)*

df, degrees of freedom; SE, standard error; LC, lethal concentration; CI, confidence interval; RR, resistance rate. Populations are presented in ascending order of resistance.

*Significant resistance ratio based on the non-inclusion of the value 1 by the respective 95% CI.

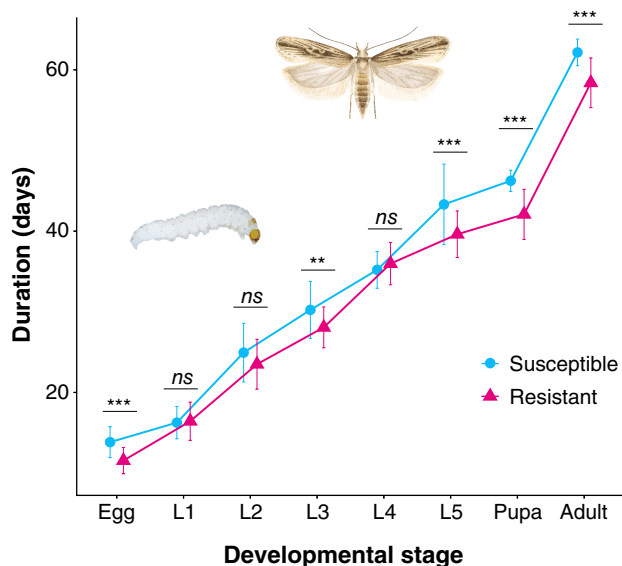


Figure 1. Cumulative developmental time for all stages of *Tecia solanivora* from the susceptible (Gualmatán) and resistant (Siachoque) populations under controlled conditions. Variation expressed as standard deviation. ns, not significant, ** $P < 0.01$, *** $P < 0.001$. Insect illustrations modified from Povolný.²⁶

the moderate levels of carbofuran resistance observed among the same populations (between 5-fold and 43-fold).

3.2 Life history traits

The near-susceptible population (i.e. marginally resistant to chlorpyrifos; from Gualmatán) and a multiple-resistant population, the one from Siachoque, were subjected to life history experiments without insecticide exposure to allow eventual detection of fitness differences between the populations likely associated with insecticide resistance to carbamates and to pyrethroids, as shown by Bacca et al.²⁸

3.2.1 Immature development

Egg-hatching was similar between both populations, with about 30% failure to hatch ($\chi^2 = 1.21$, $P = 0.27$). However, developmental time was faster in the multiple-resistant population (Fig. 1). This difference was present at each different immature stage (S1), and accumulated about a 4-day difference at adult emergence (62.1 ± 0.20 days for the near-susceptible population and 58.4 ± 0.27 days for the multiple-resistant; $\chi^2 = 196.24$, $P < 0.001$). The proportion of females emerging was also slightly biased, with a higher proportion in the multiple-resistant population (1.16 ♀/♂) and a lower proportion in the near-susceptible population (0.76 ♀/♂). Immature survival also differed between populations, with the multiple-resistant population exhibiting significantly lower survival during development than the near-susceptible population ($\chi^2 = 14.15$, $P < 0.001$) (Fig. 2).

3.2.2 Reproductive output, adult longevity and life table parameters

Fecundity was similar between females from both populations (379.60 ± 28.64 eggs female⁻¹) ($\chi^2 = 0.032$, $P = 0.85$). However, the egg-laying period was considerably different between populations (Fig. 3, Table 3). Females from the near-susceptible population started oviposition promptly after hatching, reaching a

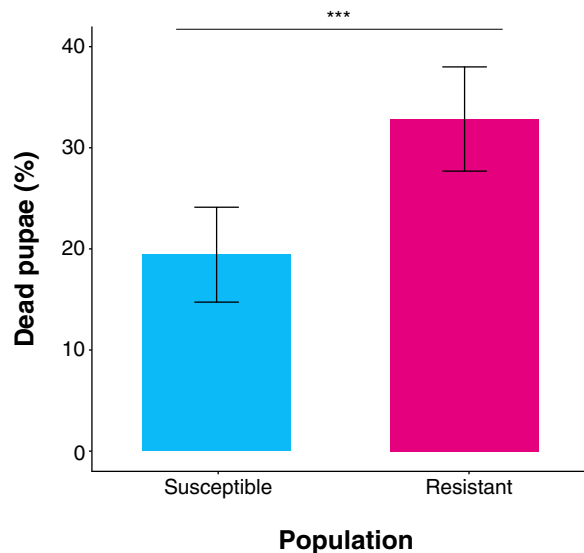


Figure 2. Mortality of pupae of the potato tuber moth *Tecia solanivora* from the susceptible (Gualmatán) and resistant (Siachoque) populations. Bars represent 95% confidence interval. $\chi^2 = 14.15$, $P < 0.001$.

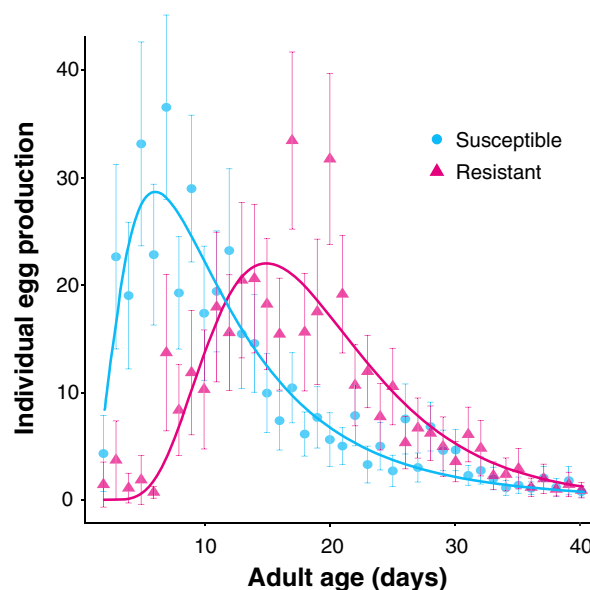


Figure 3. Daily egg production by the potato tuber moth *Tecia solanivora* from the susceptible (Gualmatán) and resistant (Siachoque) populations under controlled conditions. Adult female age calculated since emergence from cocoon. Points represent the average of eggs produced each day, variation expressed as 95% confidence intervals. The non-linear regression model selected to describe the daily egg production was the same for both populations, the log normal model with three parameters (Table 3).

peak in egg-laying around day six. In contrast, insecticide-resistant females started laying eggs later and reached a peak in egg-laying some 9 days later than the susceptible females (Fig. 3). Adult longevity was similar between populations with average values of 31 ± 1 days.

Life table parameters obtained for the near-susceptible and multiple-resistant populations of the potato tuber moth were significantly different. Generation time (T) was similar between populations (59.51 ± 0.57 days for the near-susceptible population and 60.84 ± 0.38 days for the multiple-resistant population

Table 3. Summary statistics of non-linear regression curves of reproductive output for susceptible (Gualmatán) and resistant (Siachoque) populations of the potato tuber moth *Tecia solanivora*

Model	Population	Parameter (\pm SEM)			F	Degrees of freedom (reg; error)	P	R ²
		a	b	c				
Log normal (three parameters) $y = a/x \exp(-0.5(\ln(x - c)/b)^2)$	Susceptible	28.65 \pm 0.85	0.70 \pm 0.02	6.02 \pm 0.18	454.72	3; 3416	<0.001	0.21
	Resistant	22.01 \pm 0.72	0.41 \pm 0.01	14.93 \pm 0.25	354.44	3; 4247	<0.001	0.14

Curves are depicted in Fig. 3. All equation parameters are significant at $P < 0.05$ by Student's *t* test.

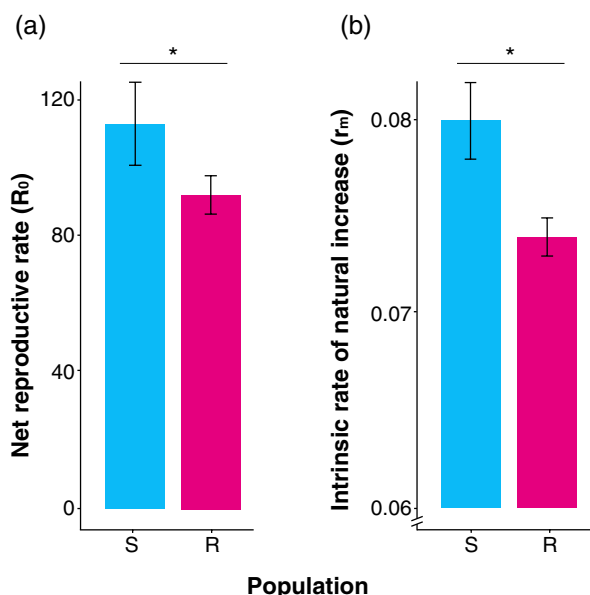


Figure 4. (a) Net reproductive rate (R_0) and (b) intrinsic rate of population growth (r_m) of an insecticide susceptible (Gualmatán) and a resistant (Siachoque) population of the potato tuber moth *Tecia solanivora*. Variation expressed as 95% confidence intervals. The asterisks indicate significant difference by Student's *t* test ($P \leq 0.06$).

($P = 0.97$), leading to similar doubling time (Dt 8.68 ± 0.32 days for the near-susceptible population and 9.31 ± 0.13 days for the multiple-resistant population ($P = 0.96$). Differences in net reproductive rate (R_0) were significant at $P = 0.06$ (Fig. 4(a)). As a consequence, the intrinsic rates of population growth (r_m) were also significantly different between populations, with the near-susceptible population exhibiting significantly higher population growth ($P = 0.037$) (Fig. 4(b)).

4 DISCUSSION

4.1 Pattern of insecticide resistance

This is the first time that carbamate resistance has been reported among populations of the potato tuber moth *T. solanivora*. Some of the populations included in our study (Iles and Ospina from Nariño, and Siachoque from Boyacá) were previously recorded as resistant to a pyrethroid insecticide,²⁸ and we also reported widespread resistance to the organophosphate chlorpyrifos, although only at low levels, and the carbamate carbofuran. However, while resistance to permethrin (earlier reported) and chlorpyrifos were relatively lower, particularly the latter, the resistance rates detected for carbofuran are higher, reaching 42-fold. These levels of carbofuran resistance are based on LC_{50} estimates,

not LC_{95} , whose reliability is much reduced, incurring in broad confidence intervals and relatively poor estimates.

Interestingly, carbofuran is not used in targeting the tuber moth, but it is used in two to three applications per crop cycle against the Andean potato weevil *Premnotrypes vorax* species that co-occurs in potato crops. Therefore, the relatively high levels of carbofuran resistance observed in the tuber moth are the result of inadvertent selection, as also reported among maize weevils and whiteflies.^{41,42} Regardless, such inadvertent selection is a pest management concern,^{43,44} and particularly so among pests of vegetable crops (e.g. Biondi *et al.*⁴⁵).

Puillandre *et al.*⁴⁶ and Torres-Leguizamon *et al.*²⁰ suggested that Colombian populations of *T. solanivora* had undergone a bottleneck process resulting in low genetic diversity. However, a recent study claimed that the species is actually experiencing a population expansion within Colombia,⁴⁷ which would likely be caused by epistasis (i.e. interaction between genes).⁴⁸ In essence, the latter could explain the ecological success of this invasive pest species.²⁰ These findings, aided by the results reported here and those of Bacca *et al.*,²⁸ suggest low genetic diversity among Colombian populations of the tuber moth and common patterns of insecticide resistance in the country. Therefore, multiple and/or cross-resistance between organophosphates and carbamates is likely common, as is altered target site resistance to pyrethroids.⁴⁹

One of the most common resistance mechanisms for carbamates reported in lepidopterans is the reduced sensibility of the enzyme acetylcholinesterase,⁵⁰ the target site of this group of insecticides and that of organophosphates as well. Nonetheless, the named enzyme can exhibit different profiles of inhibition to potential inhibitors, such as carbamates and organophosphate insecticides; thus a given population can be resistant to some carbamates but not necessarily to other carbamates or organophosphates.^{50–54}

Our results and those of Bacca *et al.*²⁸ suggest that resistance to pyrethroids and carbamates (and maybe organophosphates as well) is likely due to two distinct mechanisms indicating multiple resistance. However, the genes responsible for both mechanisms may be associated (i.e. via linkage disequilibrium), as reported in the green peach aphid *Myzus persicae* (Sulzer, 1776),⁹ which may result in an associate pattern of inheritance resembling that expected for cross-resistance. Furthermore, broad-spectrum mechanisms for detoxification such as esterases or P450^{4,5,55,56} are also likely to occur, thus conferring resistance to multiple insecticides. These possibilities need to be assessed in the potato tuber moth.

4.2 Immature development

Temperature has been regarded as the most influential factor for the development of *T. solanivora*,^{57,58} where the number of generations per year can vary from two (at 10 °C) to ten (at

25 °C).⁵⁷ However, the shorter developmental time observed for the multiple-resistant insects in our study is an exceptional case in life history strategy as the opposite has been more commonly reported.^{59,60}

Although *T. solanivora* depends in a large extent on the resources gathered during larval development,^{12,13} insects can overcome moderate shortage in nutrition in the early stages.⁶¹ Changes in developmental time in natural populations of Lepidoptera species have been associated with the host nutritional quality.⁶² However, in our controlled experiments all larvae were in homogeneous nutritional conditions and intraspecific competition, suggesting that the shorter developmental time observed in the multiple-resistant tuber moth may be an adaptation to reduce extended contact with tuber and/or soil contaminated with insecticide, which are the substrates usually treated with insecticides against the tuber moth. Such a possibility further compromises insecticide efficacy against this population and deserves attention.

The fact that the genetic diversity among Colombian tuber moth populations is rather small, and the patterns of insecticide resistance are similar among populations, suggests that this peculiarity of short developmental time associated with insecticide resistance may be widespread in the country, adding to the existing management concern with the species.

4.3 Reproductive output

Several changes in the fitness of lepidopterans have been reported as consequences of insecticide resistance or, more particularly, costs associated with insecticide resistance.⁹ Relevant life history traits such as developmental time, body mass and fecundity are potentially affected as a consequence of insecticide resistance.^{16,63–66}

The fecundities of both insecticide susceptible and resistant populations of the potato tuber moth were similar and resemble those reported in previous studies,^{23,67} but the age at which egg-laying started and peak egg production took place was earlier for the susceptible population, leading to a higher net reproductive rate. This outcome led to a higher rate of population growth in the susceptible population, as would be expected with a fitness cost associated with insecticide resistance. Again, this reproductive trade-off is likely widespread among Colombian populations of this invasive pest species, as they exhibit high genetic similarity and a similar pattern of insecticide resistance.

Although fecundity was similar between populations of the tuber moth, the resistant population exhibited an evident shift in the period of oviposition. Changes in the egg-laying period recorded in the Colorado potato beetle *Leptinotarsa decemlineata* Say, 1824 and the codling moth *Cydia pomonella* (L., 1758) have also been associated with insecticide resistance in past studies.^{16,66,68}

An oviposition peak in early adult life is the regular reproductive behavior of *T. solanivora*.²³ We hypothesize that a late-life oviposition peak in the resistant population studied could be an adaptation to compensate for the required nutrients to complete egg development. In such a case, this would help attain reproductive success,⁶⁹ but it is a hazardous strategy because the risk of mortality increases substantially in aged adults. In addition, the probability of being attacked or parasitized as an adult is comparatively larger than that of the larvae that remains protected inside the tuber.⁵⁸

In summary, pest species like the potato tuber moth *T. solanivora* exhibiting a restricted diet are more likely to evolve resistance

because they are exposed to higher pesticide concentrations and less opportunity to breed with unexposed populations.⁷⁰ Both adults and early (first instar) larvae are exposed and are therefore targets of selection for insecticide resistance. Furthermore, the restricted genetic background (i.e. low genetic diversity) and similar patterns of insecticide resistance observed in Colombian populations of the tuber moth suggest a widespread problem and common concern. However, the fitness cost associated with insecticide resistance is also likely to be common among Colombian populations of this species, encouraging the interruption and change in pattern of insecticide use to allow the existing resistance to erode with time.

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AUTHOR CONTRIBUTIONS

TB designed the experiment. LSZ and MP collected the data. YG, RNCG and TB analyzed the data. YG and RNCG wrote the manuscript, which was revised and approved by all of the authors.

CONFLICT OF INTEREST

The authors declare that they have no conflict of interest.

ETHICAL APPROVAL

All applicable national guidelines for the care and use of animals were followed.

SUPPORTING INFORMATION

Supporting information may be found in the online version of this article.

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