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Influence of a Native *Solanum tuberosum ssp. andigenum* Potato Variety on Management of the Guatemalan Potato Moth in the Venezuelan Andes

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Abstract Smallholder farmers in the Venezuelan Andes have observed that native *Solanum tuberosum ssp. Andigenum* (Andigena) potato varieties are less susceptible to damage from the invasive pest, *Tecia solanivora* P. (Lepidoptera: Gelechiidae) than improved varieties. Surprisingly, the value of using Andigena varieties in the management of *T. solanivora* remains unexplored. Field trials were established in Misinta, Venezuela, to assess *T. solanivora* damage on potatoes from an Andigena variety, 'Imilla negra', and two improved varieties, 'Andinita' and 'Unica'. The influence of intercropped Imilla negra varieties on *T. solanivora* damage and marketable yield in neighboring improved potato varieties was also assessed. While Imilla negra had significantly less *T. solanivora* damage per plant (percentage of damaged tubers) and per tuber (number of larval exit perforations) than Andinita and Unica in monoculture trials, intercropped Imilla negra did not reduce *T. solanivora* damage or increase undamaged tuber yield of improved varieties in polycultures. The results support Andean farmer knowledge on Andigena potato varieties and suggest that the proper incorporation of these varieties into potato cropping systems might be a promising strategy in managing *T. solanivora*. Nevertheless, further evaluation extending beyond a single growing season is needed to validate the findings of this study over time, as year to year variability in environmental conditions can alter host plant preference in herbivorous insects.

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Resumen Los agricultores minifundistas en los Andes venezolanos han observado que las variedades nativas de papa *Solanum tuberosum* ssp. *andígenum* (Andígena) son menos susceptibles al daño por la plaga invasiva *Tecia solanivora* P. (Lepidoptera: Gelechiidae) que las variedades mejoradas. Sorpresivamente, el valor del uso de las variedades Andígena en el manejo de *T. solanivora* permanece inexplorado. Se establecieron experimentos de campo en Misinta, Venezuela, para analizar el daño por *T. solanivora* en papas de la variedad Andígena "Imilla negra", y dos variedades mejoradas, "Andinita" y "Unica". También se evaluó la influencia de las variedades Imilla negra intercultivadas sobre el daño por *T. solanivora* y sobre el rendimiento comercial en variedades de papa mejoradas vecinas. Mientras que Imilla negra tuvo significativamente menos daño por *T. solanivora* por planta (porcentaje de tubérculos dañados) y por tubérculo (número de perforaciones de salida de las larvas) que Andinita y Unica en ensayos de monocultivo, Imilla negra intercalada no redujo el daño por *T. solanívora* o aumentó el rendimiento de tubérculo no dañado de las variedades mejoradas en policultivos. Los resultados respaldan el conocimiento del agricultor Andino respecto a las variedades Andígenas de papa, y sugieren que la correcta incorporación de estas variedades en los sistemas de cultivo de la papa pudiera ser una estrategia prometedora en el manejo de *T. solanivora*. No obstante, se requiere de evaluación posterior que se extienda más allá de un solo ciclo de cultivo, para validar lo que se encontró en este estudio sobre el tiempo, como la variabilidad de año a año en las condiciones ambientales que puedan alterar la preferencia de planta hospedante en insectos herbívoros.

Keywords *Tecia solanivora* Povolny · Genotypic diversification · Invasive pest · Traditional ecological knowledge · Integrated pest management

Introduction

The Guatemalan potato moth, *Tecia solanivora* P. (Lepidoptera: Gelechiidae), is an economically important, invasive pest of potatoes (*Solanum tuberosum* L.) in Venezuela. Larvae of *T. solanivora* bore galleries into potato tubers and are capable of reducing yields by 50 % in the field and 95 % in storage (European and Mediterranean Plant Protection Agency 2005; Mohammed et al. 2000). *Tecia solanivora* was introduced into western Venezuela in 1984 on infested seed (potato) stocks of improved potato varieties (*Solanum tuberosum ssp. Tuberosum*) from Central America (Hilje 1994). While improved potato varieties were developed by the CIP (International Potato Center, Lima, Peru) to produce high yields and to adapt to biotic and abiotic stresses (Brush et al. 1981; Thiele 1999), increased importation of seed from these varieties has facilitated the spread of *T. solanivora* into the Venezuelan Andes region, where over 70 % of domestic potato production takes place (Salas and Franco 2003).

Some potato producers in the Venezuelan Andes have maintained the tradition of cultivating native varieties of *Solanum tuberosum ssp. Andigenum* (Andigena) potatoes. Andigena potatoes are considered an important staple crop in the region, and are primarily grown for home consumption. Traditional producers also like growing Andigena varieties because of a local belief that they are less susceptible to damage from *T. solanivora* than improved varieties (Romero and Monasterio 2005). Indeed, there is substantial evidence pointing to traditional landraces as critical sources of genetic resistance to exotic pests and pathogens (Altieri 2004; Classen et al. 2014; Cole and Howard 1962). In the central and southern Andes of Peru and Argentina, native Andigena varieties have shown reduced susceptibility to economically important tuber pests, such as *Premnotrypes vorax* (Coleoptera: Curculionidae) (Brush et al. 1992; Jiménez et al. 2009). Nevertheless, there has been surprisingly little research comparing host plant preference of *T. solanivora* on improved and Andigena potato varieties.

Reduced preference of *T. solanivora* to Andigena varieties might have important pest management implications in the production of improved potato varieties. Polycultures that include non-preferred or unsuitable host plant species can significantly reduce herbivory on nearby, susceptible plant species, a phenomenon known as associational resistance (Cantelo and Sanford 1984; Khan and Pickett 2004; Ratnadass et al. 2012). Generally, associational resistance occurs when a neighboring plant species or variety enhances shared natural enemy impacts, pulls herbivores away from preferred hosts, or interferes with herbivore host plant tracking abilities, therefore reducing herbivory on a focal plant species (for a review see Barbosa et al. 2009; Jezorek et al. 2011). The latter two forms of associational resistance, described as the attractant-decoy and repellant-masking plant hypotheses, respectively (sensu Tahvanainen and Root 1972), have been documented in mixed variety potato systems in Colombia, where the incorporation of repellant and susceptible potato varieties drastically reduced oviposition rates and tuber damage by *T. solanivora* on a third focal potato variety (Gómez Jiménez and Poveda 2009).

In this study, we conducted field trials to assess whether an Andigena potato variety of the Venezuelan Andes, 'Imilla negra', is less prone to *T. solanivora* damage than improved potato varieties. We also evaluated whether improved varieties exhibit lower *T. solanivora* damage and higher marketable yields when cultivated in a polyculture with Imilla negra than when planted as monocultures.

Methods

Study System

From May to October 2011, a varietal field trial of two improved varieties 'Andinita' and 'Unica' (*S. tuberosum* ssp. *Tuberosum*) and one Andigena variety, Imilla negra (*S. tuberosum* ssp. *Andigenum*), was conducted on an eight ha farm in Misintá, Mérida State, Venezuela (latitude 8°46′ 12″N, longitude 70°54′57″W, 3500 m above sea level). Andinita and Unica potatoes require 120 to 140 days from seeding to harvest, while Imilla negra requires 140 to 180 days. Certified seed potatoes for all three varieties were obtained from the Andean farming organization PROINPA (Integrated Producers of the Páramo, Mucuchies, Venezuela). The minimum development temperature for *T. solanivora* ranges from 7 to 9 °C, with 2 generations a year at 10 °C and up to 10 generations a year at 25 °C (European and Mediterranean Plant Protection Agency 2005; Molet 2012). Adult *T. solanivora* females will leave individual eggs near the base of potato plants, and larvae spend typically around 40 to 60 days in tubers consuming potato tissue before emerging for pupation (European and Mediterranean Plant Protection Agency 2005).

Experimental Design

The varietal field trial was conducted using a randomized complete block design with six blocks and one replication per block in a 750 m^2 newly cultivated area of the farm (Fig.1a). Blocks were 25 m-long by 5 m-wide, contained five rows of potato plants spaced at 35 cm within a row and 1.1 m across rows, and were separated by a 1.5 m border of kikuyu grass (*Pennisetum clandestinum*). In each block, three "monoculture" treatments of one variety only (Andinita, Unica, and Imilla negra), and two polyculture treatments of one improved variety (Andinita and Unica) intercropped with Imilla negra were established from seed potatoes in early May 2011 (Fig. 1b).

Starting on 12 October 2011, approximately 150 days after seed potato sowing, potato plants in the first, third, and fifth row of each treatment were randomly selected for

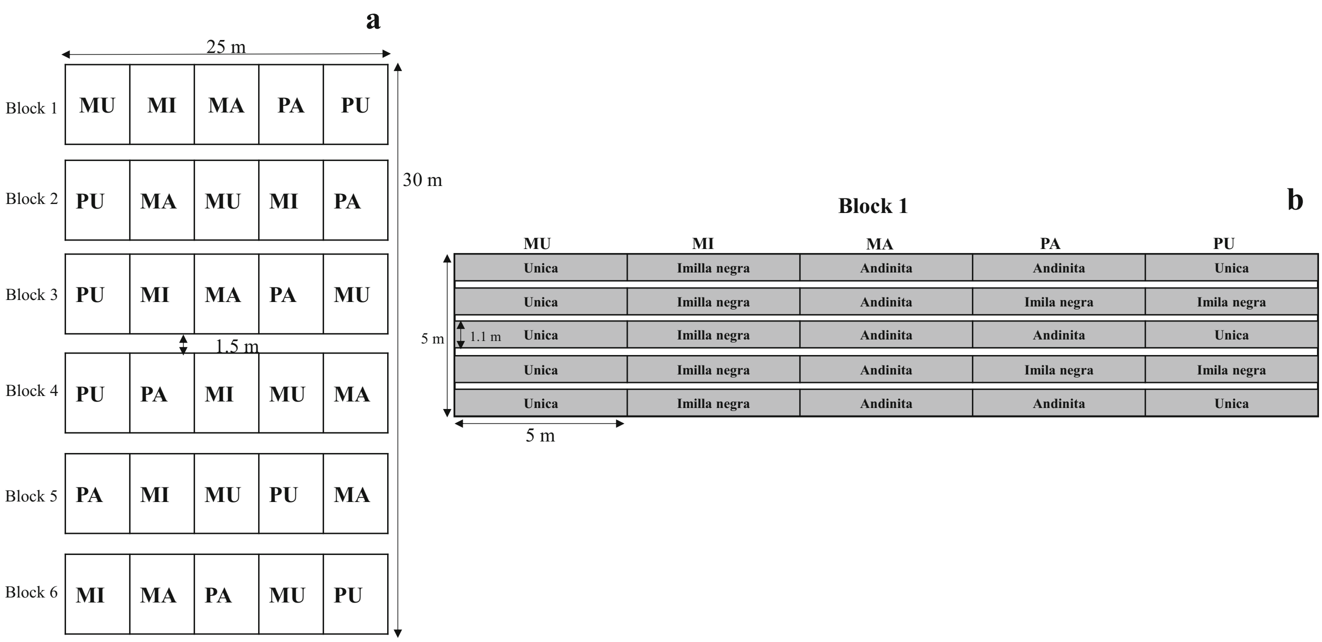

Fig. 1 Schematic of varietal field trial containing (**a**) six experimental blocks, with each block containing (**b**) five treatments established over five rows. Treatments are denoted as: MU (Monoculture Unica), MA (Monoculture Andinita), MI (Monoculture Imilla negra), PA (Polyculture Andinita), and PU (Polyculture Unica)

T. solanivora damage and marketable yield assessment (three samples per treatment, 90 total sample plants). *Tecia solanivora* damage was assessed by inspecting all tubers for signs of feeding by larvae (i.e. tunneling, mining, and exit perforations on pericarp), and estimates of damage per plant (percentage of damaged tubers) and per tuber (mean number of larval exit perforations) were calculated. Undamaged tuber yield, a commonly used parameter for marketable potato yield, was calculated for each plant by multiplying the number of undamaged tubers by mean tuber weight (sensu Poveda et al. 2010).

Statistical Analysis

A two-way multivariate analysis of variance (MANOVA) was conducted to determine if there were significant differences in *T. solanivora* damage and undamaged tuber yield between varieties (Imilla negra, Unica, and Andinita) and varietal richness (Monoculture and polyculture). Overall differences in main effects were tested using Wilk's Lambda, Pilai's Trace, Hotelling-Lawley Trace, and Roy's Greatest Root. Interactions between main effects and univariate significances of simple

Table 1 Overall MANOVA tests of *T. solanivora* damage and undamaged tuber yield between the main effects (Variety and Varietal richness) and interaction term (Variety x Varietal Richness)

Main effect	MANOVA test	F	df1	df2	*P*-value
Variety	Wilks-Lambda (Λ)	7.37	14	170	All <0.001***
	Pilai's Trace	5.92	14	172	
	Hotelling-Lawley Trace	8.93	14	133	
	Roy's Greatest Root	17.38	7	86	
Varietal richness	Wilks-Lambda (Λ)	All 1.08	All 7	All 85	All 0.38
	Pilai's Trace				
	Hotelling-Lawley Trace				
	Roy's Greatest Root				
Variety x Varietal richness	Wilks-Lambda (Λ)	0.83	14	170	0.64
	Pilai's Trace	0.84	14	172	0.63
	Hotelling-Lawley Trace	0.82	14	133	0.64
	Roy's Greatest Root	1.06	7	86	0.40

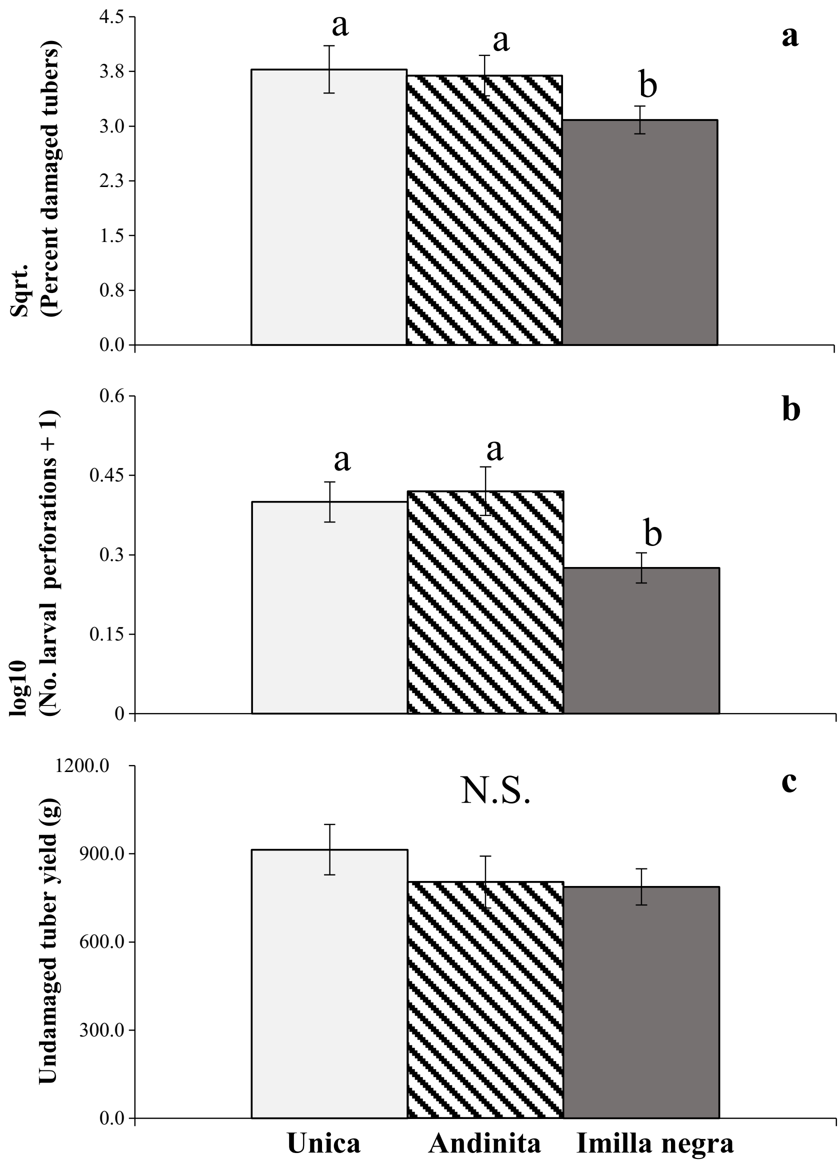

Fig. 2 Mean **(a)** percentage of damaged tubers per plant (square root transformed), **(b)** number of larval exit perforations per tuber (log 10 transformed), and **(c)** undamaged tuber yield between monoculture treatments of Unica, Andinita, and Imilla negra potatoes. Vertical bars are 95 % confidence intervals, with significant differences between varieties indicated by different lowercase letters as determined by Tukey's post-hoc tests ($\alpha = 0.05$). Transformed means and 95 % confidence intervals for percent damaged tubers and larval exit perforations are reported here

main effects were also evaluated. Tukey-adjusted post-hoc contrasts were used to compare *T. solanivora* damage and undamaged tuber yield between 1) all three varieties in monoculture and 2) improved varieties in monoculture vs. polyculture treatments with Imilla negra. A square root transformation on percent damaged tubers and log base 10 transformation on number of larval exit perforations were necessary to satisfy variance and normality assumptions for MANOVA. All statistical analyses were carried out using SAS version 9.3 (SAS Institute 2007).

Results and Discussion

All four MANOVA tests (i.e., Wilk's Lambda, Pilai's Trace, Hotelling-Lawley Trace, and Roy's Greatest Root) revealed significant overall differences in *T. solanivora* damage between varieties (Table 1). *T. solanivora* damage per plant (Percent damaged tubers, Imilla negra vs. Unica and Andinita: $t = 3.23$, $p = 0.01$) and per tuber (Larval exit perforations, Imilla negra vs. Unica and Andinita: $t > 4.74$, $p < 0.001$) were significantly lower on Imilla negra potatoes than on Unica and Andinita (Fig. 2a, b; Table 2). Nevertheless, undamaged tuber

Table 2 Univariate results of *T. solanivora* damage per plant (percent damaged tubers), per tuber (number of larval exit perforations), and undamaged tuber yield between varieties

Tuber variable	MS	F	df1	df2	*P*-value
Percent damaged tubers per plant	4.35	3.23	10	91	0.001**
No. of larval exit perforations per tuber	0.15	3.62	10	91	<0.001***
Undamaged tuber yield	6.93E5	3.56	10	90	0.41

yield did not significantly differ between Imilla negra, Unica, and Andinita varieties (Undamaged tuber yield, all monoculture variety comparisons: $t > 2.97$, $p > 0.41$, Fig. 2c), which was likely driven by an over two-fold difference in mean tuber weight between improved varieties and Imilla negra (Fig. 3). The results of this trial provide evidence in support of local farmer knowledge that Andigena potato varieties are less susceptible to *T. solanivora* damage than improved varieties.

Our study is not the first to report increased resistance *of S. tuberosum* ssp. *Andigenum* varieties to economically important exotic pests and pathogens. Imilla negra and at least seven other varieties of Andigena potatoes are resistant to the fungal pathogen *Rhizoctonia* (Jiménez et al. 2009). More commonly, however, Andigena varieties have been used as a gene source for the development of pest and pathogen-resistant *S. tuberosum* ss*p. Tuberosum* varieties. Efforts aimed at regulation of the potato cyst nematode *Globodera rostochiensis*, for instance, include the development of *S. tuberosum* ss*p. Tuberosum* varieties containing the H1 resistance gene from Andigena potatoes (Dias et al. 2012; Osypchuk et al. 2002). Germplasm evaluations of Andigena potatoes have also revealed possible resistance to *Phoma exigua*, the causal agent of potato gangrene in storage, and the potato root eelworm, *Heterodera rostochiensis* (Fischl 1991; Toxopeus and Huijsman 1952).

We also tested whether intercropping a non-preferred Andigena variety such as Imilla negra can reduce *T. solanivora* damage and improve marketable yield of improved varieties. MANOVA results indicated, however, that neither *T. solanivora* damage nor undamaged tuber yield significantly differed in Andinita and Unica varieties when they were intercropped with Imilla negra versus when planted as monocultures (*T. solanivora* damage; Monoculture Andinita vs. Polyculture Andinita: $t > 2.97$, $p > 0.41$, Monoculture Unica vs. Polyculture Unica: $t > 0.30$, $p > 0.29$). While these findings might not support the strategy of intercropping Imilla negra as a means of reducing *T. solanivora* damage on nearby improved varieties, Andigena potatoes remain an important source of household subsistence for traditional potato producers and require fewer pesticide applications than their improved counterparts. Furthermore, it remains unclear whether the incorporation of Imilla negra potatoes under other spatial configurations (i.e., surrounding borders, within-field plots, strip-cropped rows) may lead to different

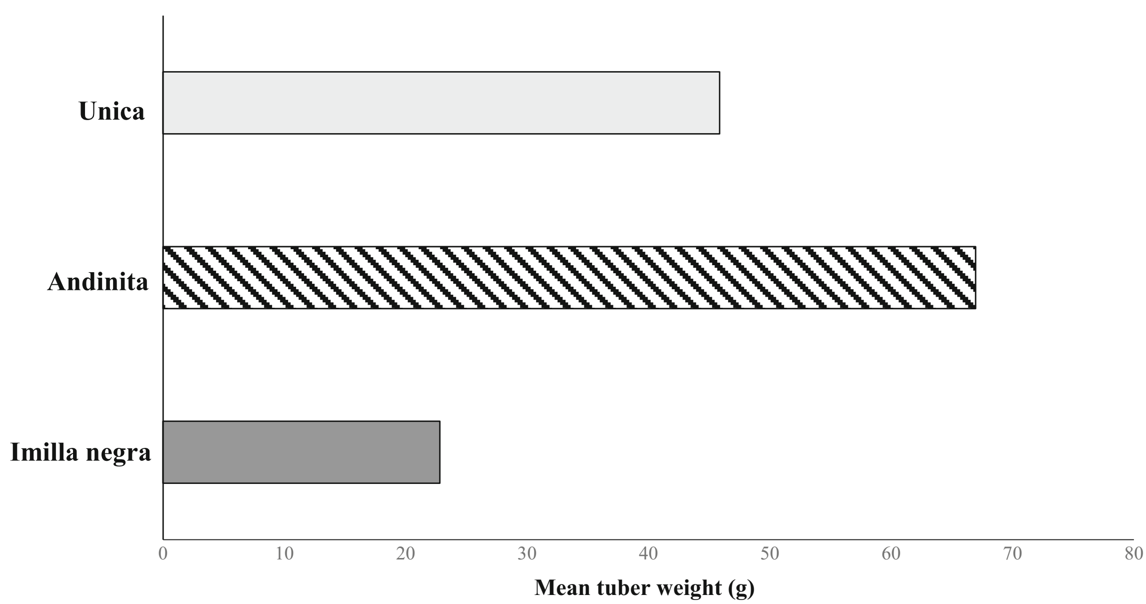

Fig. 3 Mean tuber weight of Unica, Andinita, and Imilla negra potatoes

outcomes regarding *T. solanivora* damage on nearby conventional varieties (Barbosa et al. 2009).

Our findings suggest that associational resistance interactions did not occur between Imilla negra and the intercropped improved varieties, i.e. Imilla negra did not alter the susceptibility of improved varieties to *T. solanivora* (Johnson 2008; Tooker and Frank 2012). While the presence of an unpalatable neighbor can reduce the susceptibility of crop species or varieties to herbivory, the likelihood of associational resistance occurring in diversified cropping systems depends on multiple plant and herbivore traits not tested here. In our varietal trials, we observed that Imilla negra plants produced abundant aboveground biomass and tended to overcrowd neighboring rows of Unica and Andinita plants, potentially creating a structurally complex microhabitat for natural enemies. While structural complexity can increase the establishment of ground dwelling natural enemies, it can also reduce the ability of active foraging predators and parasitoids to find prey (Legrand and Barbosa 2003; Rivera and Burrack 2012). Furthermore, specialist herbivores with well-developed host plant tracking and dispersal abilities are less likely to have difficulty locating host plants that are surrounded by unpalatable species than generalist pests (Banks 1998; Harmon et al. 2003). Given that *T. solanivora* is a highly specialized pest species capable of directed, albeit fairly weak flight, a polyculture containing a single resistant variety may be insufficient in reducing the detection of susceptible varieties to ovipositing females (Dangles et al. 2009; European and Mediterranean Plant Protection Agency 2005; Karlsson et al. 2009). A recent study, for instance, found that *T. solanivora* oviposition and damage on a *S. tuberosum* ss*p. Tuberosum* variety, 'Pardo Pastusa', was only lowered when paired with both an attractant and repellant variety, but not lowered when paired with only an attractant or repellant variety alone (Gómez Jiménez and Poveda 2009).

However, it is important to note that because environmental conditions can be highly variable from one growing season to the next, it will be necessary to evaluate host preference of *T. solanivora* to Andigena potato varieties over multiple growing seasons. Indeed, host plant tracking abilities and oviposition behavior in herbivorous insects is greatly influenced by climatic factors (Foster and Harris 1997). Given that climatic conditions were relatively stable over the course of the study and consistent with typical March to October weather in the Venezuelan Andes, it is unlikely that the results were unique to the study year. Nevertheless, it will be important to further evaluate the validity of the results through longer term studies testing preference of *T. solanivora* to Andigena and improved varieties.

Identifying an effective method for managing *T. solanivora* through the integration of Andigena varieties in Andean potato cropping systems remains a complex yet potentially promising challenge. We suggest that future research should focus on 1) discerning the mechanisms of *S. tuberosum* ssp. *Andigenum* resistance to *T. solanivora* (i.e., reduced palatability, defense compounds, semiochemicals and natural enemy recruitment) through laboratory studies, and 2) understanding how spatial and temporal factors of *S. tuberosum* ssp. *Andigenum* cultivation influence the incidence of *T. solanivora* in potato fields. Both suggested lines of research can yield information that is germane to the design of resistant and resilient agroecosytems that are less susceptible to pest invasion. The cultivation of repellant crop "borders" around susceptible crops, for instance, has been shown to effectively reduce the establishment of specialist herbivores (Bottrell et al. 1998; Shelton and Badenes-Perez 2006).

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