Natural selection drives chemical resistance of *Datura stramonium*

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Plant resistance to herbivores involves physical and chemical plant traits that prevent/diminishes damage by herbivores and hence, may promote coevolutionary arm-races between interacting species. Although *Datura stramonium's* concentration of tropane alkaloids is under selection by leaf beetles, it is not known whether chemical defense reduces seed predation by the specialist weevil, *Trichobaris soror*, and if it is evolving by natural selection. We measured infestation by *T. soror* as well as the concentration of the plants' two main tropane alkaloids in 278 *D. stramonium* plants belonging to 31 populations in central Mexico. We assessed whether the seed predator exerted preferences on the levels of both alkaloids and whether they affect plant fitness. Results show great variation across populations in the concentration of scopolamine and atropine in both leaves and seeds of plants of *D. stramonium*, as well as in the intensity of infestation and the proportion of infested fruits by *T. soror*. The concentration of scopolamine in seeds and leaves are negatively associated across populations. We found that scopolamine concentration increases plant fitness. Our major finding was the detection of a positive relationship between the population average concentrations of scopolamine with the selection differentials of scopolamine. Such spatial variation in the direction and intensity of selection on scopolamine may represent a coevolutionary selective mosaic. Our results support the view that variation in the concentration of scopolamine among-populations of *D. stramonium* in central Mexico is being driven, in part, by selection exerted by *T. soror*, pointing an adaptive role of tropane alkaloids in this plant species.

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Adán Miranda–Pérez [1], Guillermo Castillo [1], Johnattan Hernández-Cumplido [2], Pedro L. Valverde[3], María Borbolla [1], Laura L. Cruz [1], Rosalinda Tapia-López [1], Juan Fornoni [1], César M. Flores–Ortiz [4] and Juan Núñez–Farfán [1]*

[1] Laboratorio de Genética Ecológica y Evolución, Departamento de Ecología Evolutiva, Instituto de Ecología, Universidad Nacional Autónoma de México, México, Distrito Federal, México

[2] Institute of Biology, University of Neuchâtel (UNINE), Neuchâtel, Switzerland

[3] Departamento de Biología, Universidad Autónoma Metropolitana–Iztapalapa, México, Distrito Federal, México

[4] UBIPRO, Facultad de Estudios Superiores Iztacala, Universidad Nacional Autónoma de México, Tlalnepantla, Estado de México, México.

*Corresponding author: Juan Núñez-Farfán, Laboratorio de Genética Ecológica y Evolución, Departamento de Ecología Evolutiva, Instituto de Ecología, Universidad Nacional Autónoma de México, Apartado Postal 70-275. Distrito Federal, 04510, México, E-mail: farfan@unam.mx

Introduction

The coevolutionary process involves reciprocal selection-adaptation between interacting species through time (Dawkins & Krebs, 1979; Thompson, 1999; Thompson, 2005). This adaptation and counter-adaptation phenomenon could result in a coevolutionary arms race, a process of offense-defense (Dawkins & Krebs, 1979). A coevolutionary relationship between plants and herbivores may generate symmetrical or asymmetrical selective pressures between interacting species. These selective pressures may be different spatially and could produce a geographic structure of interactions (Forde, Thompson & Bohannan, 2004; Gomulkiewicz *et al*., 2002; Nuismer, Thompson & Gomulkiewicz, 2000; Thompson, 1999; Thompson, 2005). In some locations the interacting species exert reciprocal selection pressures to one another (coevolutionary hot spots), whereas in other locations reciprocal selection is highly asymmetric (coevolutionary cold spots) (Gomulkiewicz *et al*., 2002; Nuismer, Thompson & Gomulkiewicz, 2000; Thompson, 1999; Thompson, 2005).

A coevolutionary arms race between herbivores and plants may be favored in specialized interactions as in the case of insects that detoxify specific compounds (Janzen, 1969; Janzen, 1973; Schoonhoven, Van Loon & Dicke, 2005). For instance, the aphid *Macrosiphum albifrons* is adapted to consume *Lupinus angustifolius* with a low content of alkaloids (Philippi *et al*., 2015); however, dietary specialist herbivore insects may also be adapted to tolerate secondary metabolites of their host plants without switching to other different host plants (Laukkanen *et al*., 2012). In *Arabidopsis thaliana,* the abundance of two aphid herbivore species is correlated to a genetic polymorphism of the plant´s resistance locus. This polymorphism is under selection due to changes in population size of the two aphid species (Züst *et al*., 2012).

Host-parasite systems, that exert reciprocal selection pressures, offer the opportunity to assess the asymmetry in selection pressures and the potential to produce adaptation (Greischar & Koskella, 2007). Local adaptation may produce population differentiation as a by-product of natural selection (Kawecki & Ebert, 2004). This process is well illustrated by the weevil *Curculio camelliae* (Coleoptera: Curculionidae) that parasitizes the fruits of *Camellia japonica* (Theaceae) (Iseki, Sasaki & Toju, 2011; Toju, 2007; Toju, 2009; Toju & Sota, 2006). The fruits of *C. japonica* are capsules with a thick pericarp, dehiscent, with three locules and one seed per cavity (Okamoto, 1988). Females of *C. camelliae* perforate the thick pericarp with its long *rostrum*, modified labial cavity in insects (Resh & Cardé, 2009), and oviposit on the seeds (Toju, 2007). A successful weevil infestation, or oviposition, depends on the phenotypic match between the rostrum length and pericarp thickness. These two traits that mediate the interaction vary geographically and are under selection (Toju, 2007; Toju, 2009; Toju & Sota, 2006). Some evidence, however, indicates that these phenotypic characteristics may also vary according to abiotic factors, i. e. the latitude (Iseki, Sasaki & Toju, 2011). Furthermore, infestation by the weevil *C. camelliae* increases at higher-altitude localities and its obligated host plant decreases its resistance (Toju 2009). In the *C. camelliae*-*C. japonica* system, natural selection acts on pericarp thickness that is a physical barrier that prevents infestation by weevils (Toju, 2007; Toju, 2009; Toju, 2011; Toju & Sota, 2006).

In the annual herb *Datura stramonium,* tropane alkaloids function either as resistance characters preventing foliar damage by herbivores and/or as phagostimulants to them (Castillo *et al*., 2013; Castillo *et al*., 2014; Shonle & Bergelson, 2000). Evidence shows that alkaloid concentration in *D. stramonium* varies across populations (Castillo *et al*., 2014) and that such differentiation in chemical defense could be adaptive (Castillo *et al*., 2015). In some populations,

dietary specialist and generalist folivores select against atropine concentration, whereas scopolamine is positively selected selected by the dietary specialist folivore *Lema daturaphila* and by the generalist grasshopper *Sphenarium purpurascens* (Castillo *et al*., 2014). Fruits of *D. stramonium* are parasitized by *Trichobaris soror* (Coleoptera: Curculionidae) that reduces plant fitness by consuming the seeds (Cabrales-Vargas, 1991; Cruz, 2009; De-la-Mora, Piñero & Núñez-Farfán, 2015). However, to what extent alkaloids of *D. stramonium* could affect infestation by the seed predator is not known. Here, we analyzed the relationship between tropane alkaloids produced by *D. stramonium* and infestation by the specialized seed predator *T. soror* across multiple populations in central Mexico. We aimed to determine whether *D. stramonium*'s tropane alkaloids prevent infestation by *T. soror*. Specifically, we addressed the following questions. 1. Are alkaloids resistance characters that prevent/reduce infestation by weevils? 2. Do seed predators exert natural selection upon plant´s alkaloids concentration? And 3. Do variation of both alkaloid concentration and infestation by weevils across populations is correlated to the localities' environmental conditions? (*v. gr*., Toju, 2009).

Materials and methods

Study system

The weevil *Trichobaris soror* (Coleoptera: Curculionidae) is intimately associated to the life cycle of *D. stramonium* (Bello-Bedoy, Cruz & Núñez-Farfán 2011a, Borbolla, 2015; Cabrales-Vargas, 1991). *Trichobaris soror* is distributed mainly in central Mexico (Barber, 1935; De-la-Mora, Piñero & Núñez-Farfán, 2015); adult weevils feed on leaves, calyx and floral tissues of *D. stramonium*. After mating, females oviposit at the base of developing fruits. Their larvae feed exclusively on immature seeds inside the developing fruit where

90 they build tunnels with their own feces. Larvae pupate in the fruit and sometimes are
91 parasitized by wasps. The weevils hibernate inside the fruit of *D. stramonium* until the
92 next rainy season (Bello-Bedoy, Cruz & Núñez-Farfán 2011a, Borbolla, 2015; Cabrales-
93 Vargas, 1991).

94 Besides the seed predator, *D. stramonium* (Solanaceae) is preyed upon by
95 specialist leaf-beetles (*Lema trilineata* and *Epitrix parvula*, Coleoptera: Chrysomelidae).
96 This weed species has been widely studied in relation to its resistance characters
97 (alkaloids, leaf trichomes) against these leaf herbivores (Bello-Bedoy & Núñez-
98 Farfán, 2011b; Cabrales-Vargas, 1991; Carmona & Fornoni, 2013; Castillo *et al*., 2013;
99 Castillo *et al*., 2014; Núñez-Farfán & Dirzo, 1994; Shonle & Bergelson, 2000; Valverde,
100 Fornoni & Núñez-Farfán, 2001). However, it is unknown if chemical defense of *D.*
101 *stramonium* prevents the infestation by the weevil *T. soror*.

102

103 *Sampled populations*

104 During the reproductive season of *D. stramonium* (September-November) in 2007, we
105 sampled different populations across Central Mexico. We collected an average of 30
106 plants from 31 populations (Fig. 1, Table S1). For each plant, all mature fruits were
107 collected and individually bagged and labeled. Before opening, the width and length of
108 each fruit was measured to calculate its volume with the equation:

109

110 $$V = \left(\frac{4}{3}\right)(\pi)(length)\left(\left(\frac{width}{2}\right)^2\right)$$

111

112 We estimated the number of expected seeds by multiplying the volume by 0.026
113 (Fornoni, Valverde & Núñez-Farfán, 2004). In the laboratory, we opened the fruits to
114 determine the infestation, by counting the weevils. Also, for each fruit we counted the
115 number of remaining, sound, seeds after predation.

116

117 *Seed predator´s infestation measures*
118 We measured the intensity of infestation by *T. soror* to *D. stramonium* as the number of
119 weevils divided by the number of fruits per plant (Greischar & Koskella, 2007). Also, we
120 measured the infestation as the proportion of infested fruits per plant.
121

122 *Alkaloid concentration*
123 We quantified the concentration of leaf atropine and scopolamine per plant (Boros et
124 al. 2010), by means of high-performance liquid chromatography (HPLC), following
125 Castillo et al. (2013). We obtained the average leaf alkaloid concentration from a
126 sample of 8-10 plants per population. In order to assess if leaf and seeds alkaloid
127 concentration are correlated, we measured alkaloids of mature seeds in a subsample of
128 119 plants of 14 populations (Table S2).
129

130 *Characterization of environmental variables*
131 In order to control for some concomitant environmental variation, the values of mean annual
132 temperature and precipitation for the 31 studied populations of the *D. stramonium* were obtained
133 from Worldclim (Hijmans & Graham, 2006). We characterized each population by calculating

134 the Lang´s aridity index (Rehman, 2010), as the ratio of population mean annual precipitation
135 and mean annual temperature. Values between 0-20 correspond to deserts, 20-40 arid habitats,
136 40-60 wet type steppes, 60-100 wet woodlands and 100-160 wet forests (Perry, 1986).

137

138 *Statistical analyses*

139 We assessed the among-population variation in the intensity of infestation, the proportion of
140 infested fruits by *T. soror*, and the concentration of atropine and scopolamine in seeds and in
141 leaves, using generalized linear model (GzLM), assuming a gamma distribution and a log link
142 function. Our hypothesis is that infestation by the seed predator does not vary among
143 populations of *D. stramonium*.

144 The relationship between the concentration of atropine and scopolamine in both leaves
145 and seeds was tested through generalized linear mixed models (GzLMM), with a gamma
146 distribution, a log link function and population as a random factor. Data were obtained from
147 individual plants from a subsample of 14 populations. In order to assess the effect of the seed
148 predator on plant fitness, we performed a GzLMM of the number of remaining sound seeds, as
149 estimator of fitness, as a function of the proportion of infested fruits per plant and population as a
150 random factor. Again, we assumed a gamma distribution and a log link function. Similarly, we
151 tested if the concentration of atropine and scopolamine in leaves increases plant individual
152 fitness. We assumed the population × proportion of infested fruits interaction as a random
153 factor.

154 Selection differentials (*S*) that account for direct and indirect selection acting on a trait
155 were calculated through Pearson correlation coefficient for each population (Lande &

Arnold, 1983). The concentration of atropine and scopolamine in seeds and leaves was standardized ($x' = \frac{(x-\mu)^2}{\sigma}$). As a proxy of plant fitness we used the estimated number of seeds per plant (other examples in Kingsolver *et al*., 2001). The relative fitness was defined as the ratio between individual fitness and population average fitness. Selection differentials were estimated for each population by correlating alkaloid concentration standardized (atropine or scopolamine) with relative fitness (such in Sobral *et al*., 2013; Sobral *et al*., 2015).

In order to explore the effect of selection exerted by the seed predation and environmental variables on the concentrations of scopolamine and atropine in both leaves and seeds, across populations of *D. stramonium*, we performed generalized linear models (GzLM) (such in Herrera, Castellanos & Medrano, 2006; Sobral *et al*., 2015). In each model we included the selection differential of the corresponding alkaloid, latitude, longitude, altitude, and Lang's index of each population. We assumed a gamma distribution (log link function) for alkaloid concentration in leaves, and a Gauss inverse (identity link function) for seeds. We selected the models with lowest corrected AIC values, namely those that explain better the relationship between the variables and consider the sample size (Akaike, 1974; SPSS, 2011). Statistical analyzes were performed with SPSS v20.0 statistical package (SPSS, 2011).

Results

We detected wide variation in concentration of scopolamine and atropine in leaves (Fig. 2; Table 1) and seeds (Fig. 3; Table 1) across populations of *D. stramonium*. The proportion of infested fruits as well as the intensity of infestation by *T. soror* to plants of *D. stramonium*

varied significantly among populations (Fig. 4; Table 1). Variation in the average proportion of infested fruits ranged from zero (populations Coatepec, Huitzuco and Jalapa) up to 90% (populations Teotihuacan and Tlaxiaca; Fig. 4). The average intensity of infestation by *T. soror* varies from populations without infestation up to those with 5 weevils per fruit, per plant.

The concentration of atropine and scopolamine in leaves is positive and significantly related (N = 117, *Estimate* = 0.289, *S.E.* = 0.055, $t = 5.285$, $P < 0.0001$, AICc = 306), while the correlation of scopolamine in leaves and seeds is negative (N = 117, *Estimate* = -1.29, *S.E.* = 0.484, $t = -2.666$, $P = 0.009$, AICc = 305.279). Similarly, the concentration of scopolamine in leaves and atropine in seeds are negatively related (N = 117, *Estimate* = -1.061, *S.E.* = 0.481, $t = -2.206$, $P = 0.029$, *AICc* = 307.407).

The number of sound remaining seeds per plant showed a negative relationship with the proportion of infested fruits *T. soror* (N = 278; *Estimate* = -0.629, S.E. = 0.266; $t = -2.367$; $P = 0.019$; AICc = 832.46). We found that the number of remaining sound seeds shows a positive relationship with both scopolamine concentration in leaves (N = 278; *Estimate* = 0.200, S.E. = 0.076; $t = 2.639$; $P = 0.009$; AICc = 886.85) and seeds (N = 119; *Estimate* = 13.56, S.E. = 3.56; $t = 3.81$; $P < 0.0001$; AICc = 403.32).

A GzLM of the population average of scopolamine concentration in leaves is positively related to the selection differential (*S*) of leaf scopolamine (Table 2, Fig. 5A). The same result, although marginally significant, was detected for scopolamine in seeds.

In the case atropine concentration in seeds, the GzLM indicates a positive and highly significant relationship with the Lang´s aridity index; atropine concentration in leaves is marginally significant in its relationship with Lang´s aridity index (Table 2, Fig. 5B).

201

202 **Discussion**

203 Populations of *D. stramonium* vary in the concentration of alkaloids in leaves. This result is
204 in agreement with the study of Castillo *et al.* (2013). Here, we found that populations of *D.*
205 *stramonium* also vary in the concentration of alkaloids in seeds, in the intensity of
206 infestation, as well as in the proportion of infested fruits by *T. soror*. The concentration of
207 scopolamine in seeds and leaves is negatively associated across populations. Although such
208 a pattern was not detected for atropine, the concentration of scopolamine and atropine in
209 leaves, positively covary across populations. Remarkably, we detected that scopolamine
210 concentration in both leaves and seeds enhances individual plant fitness. Our major finding
211 was the detection of a positive relationship between the population average concentration of
212 scopolamine in both leaves and seeds with the selection differentials of scopolamine. This
213 implies that natural selection explains the among population variation in scopolamine
214 concentration. Thus, *T. soror* is driving, at least in part, the variation in chemical defense in
215 *D. stramonium* (Castillo *et al*., 2015).

216 A previous study has reported that scopolamine plays a role in the interaction
217 between *D. stramonium* and its main folivore insects in central Mexico (Castillo *et al*.,
218 2014). Here, we found that among-populations of *D. stramonium*, plants with higher
219 concentration of scopolamine in leaves had a higher number of remaining sound seeds. This
220 suggests that scopolamine acts as a defense character against *T. soror*, resulting in fewer
221 consumed or damaged seeds. A similar trend has been found in the hemiparasitic plant
222 *Castilleja indivisa* (Adler, 2000), where the alkaloid lupanine, obtained from its host plant,
223 *Lupinus texensis*, reduces damage to its flowers by herbivores and increases visitation by

pollinators, thus enhancing plant fitness, measured as the number of seeds.

The fact that the concentration of scopolamine in leaves and seeds are negatively correlated, probably pointing an allocation trade-off (Kariñho-Betancourt *et al*., 2015), this does not preclude that scopolamine concentration in leaves had a negative effect on the seed predator. Adult females and males of *T. soror* courtship, mate, and feed on *D. stramonium* leaves (J. Núñez-Farfán, *personal observation*). When feeding, adult weevils produce small holes on the leaf blade, and sometimes damage can be severe (Cabrales-Vargas, 1991). Thus, it is likely that *T. soror*'s females, while feeding, might "assess" the chemical resistance level of a plant (i.e., atropine/scopolamine concentration in leaves) and select which plants are suitable to oviposit. This would result in lower or null oviposition in those plants with high concentration of scopolamine in leaves. Some evidence in this line shows a close relationship between *Trichobaris* and *Datura*. For instance, *Trichobaris bridwelli* oviposits preferentially on *D. stramonium* rather than on tobacco plants (*Nicotiana tabacum*) (Cuda & Burke, 1991), since *T. bridwelli* does not tolerate the pyridine alkaloids of tobacco (Cuda & Burke, 1991). On the other hand, Diezel *et al*. (2011) have experimentally demonstrated that *T. mucorea*, a species that burrows into the stems of *Nicotiana attenuata*, increases infestation on transgenic plants of *N. attenuata* where the chemical defenses (jasmonic acid and nicotine) were silenced.

The role of scopolamine as defense against herbivory in *D. stramonium* is supported by the findings of Castillo *et al*., (2014). In such study, they detected positive selection on scopolamine concentration in leaves in two populations of *D. stramonium,* one preyed upon by the dietary specialist *Lema daturaphila*, and the other by the dietary generalist *Sphenarium purpurascens*. However, also negative selection on scopolamine was detected in

247 a third population of *D. stramonium* preyed by *L. daturaphila*. Thus, the resistance role of
248 tropane alkaloids of *D. stramonium* varies according to the type of herbivore and the tissue
249 they consume, as well as the environmental conditions of populations (Castillo *et al*., 2014).
250 Further studies are needed to determine the independent and join selective effects of
251 folivores and seed predators on the concentration of scopolamine in seeds and leaves of *D.*
252 *stramonium*.

253 The GzLM shows that atropine in seeds covaries positively with the Lang´s index. That is
254 to say, populations of dry environments have less atropine concentration. It has been reported that
255 alkaloid production may be water limited, decreasing in concentration in dry environments
256 (Baricevic *et al*., 1999). In the interaction between *Curculio camelliae-Camellia japonica*, the
257 expression of defense is also affected by the habitat's environmental conditions; infestation by the
258 weevil was higher at high altitudes, where the fruits of *C. japonica* trees have thinner pericarps
259 (Toju, 2009). Thus, the evolution of chemical defense against herbivores in *D. stramonium* can
260 also be environmentally conditioned.

261 We found evidence of natural selection on chemical resistance of *D. stramonium* since
262 higher scopolamine concentration increases plant fitness. The GzLM analysis revealed a positive
263 relationship between the population average concentrations of scopolamine in both leaves and
264 seeds with their selection differential of scopolamine. This relationship suggests that the among-
265 population variation in chemical defense of *D. stramonium* is molded by *T. soror*. Thus,
266 populations of *D. stramonium* vary in the direction and strength of selection on chemical defense,
267 an expectation of the geographic mosaic of coevolution (i.e., hot spots and cold spots; Thompson,
268 2005). Previous evidence has demonstrated that leaf herbivores exert selection pressures over
269 physical and chemical defenses of *D. stramonium* (Valverde, Fornoni & Núñez-Farfán, 2001;

Castillo *et al*., 2014). This is the first evidence that seed predators also exert a significant selective pressure on chemical defense of *D. stramonium*.

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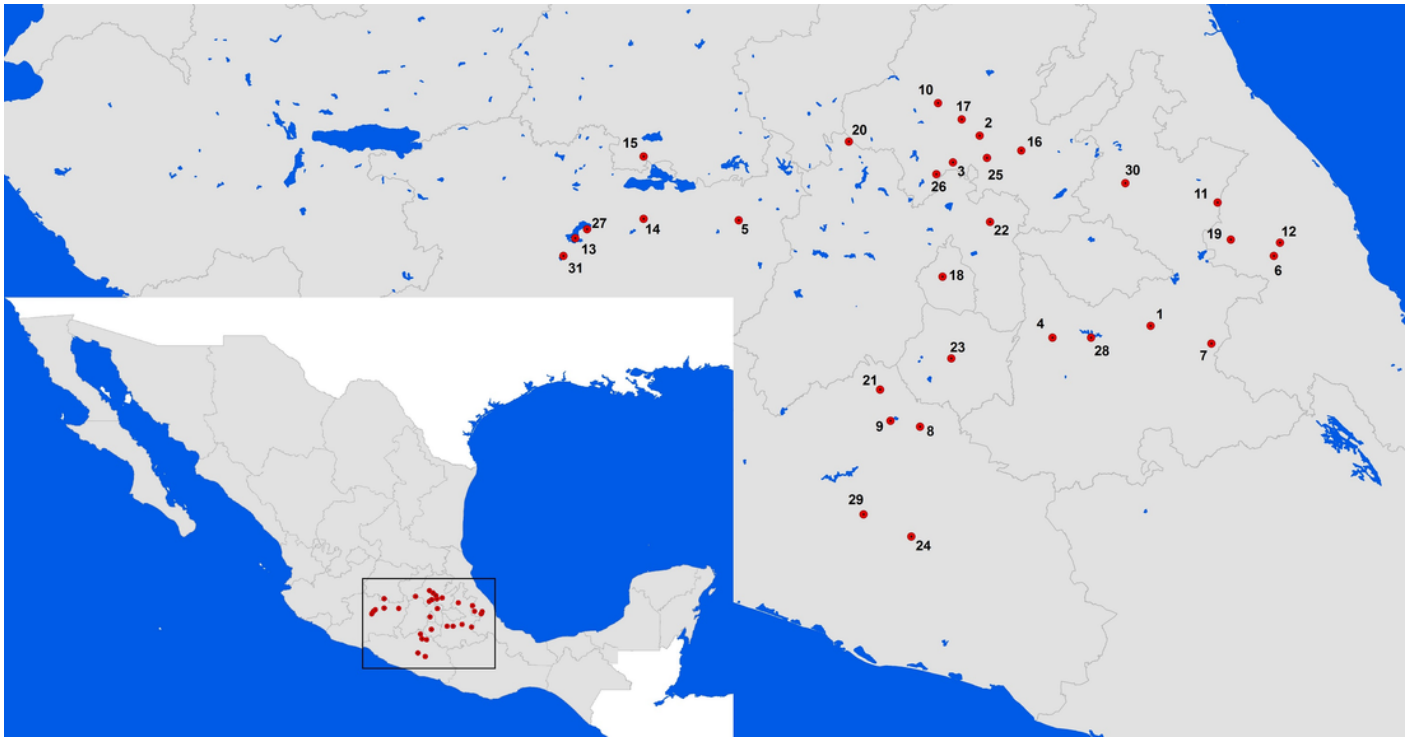
1

Figure 1

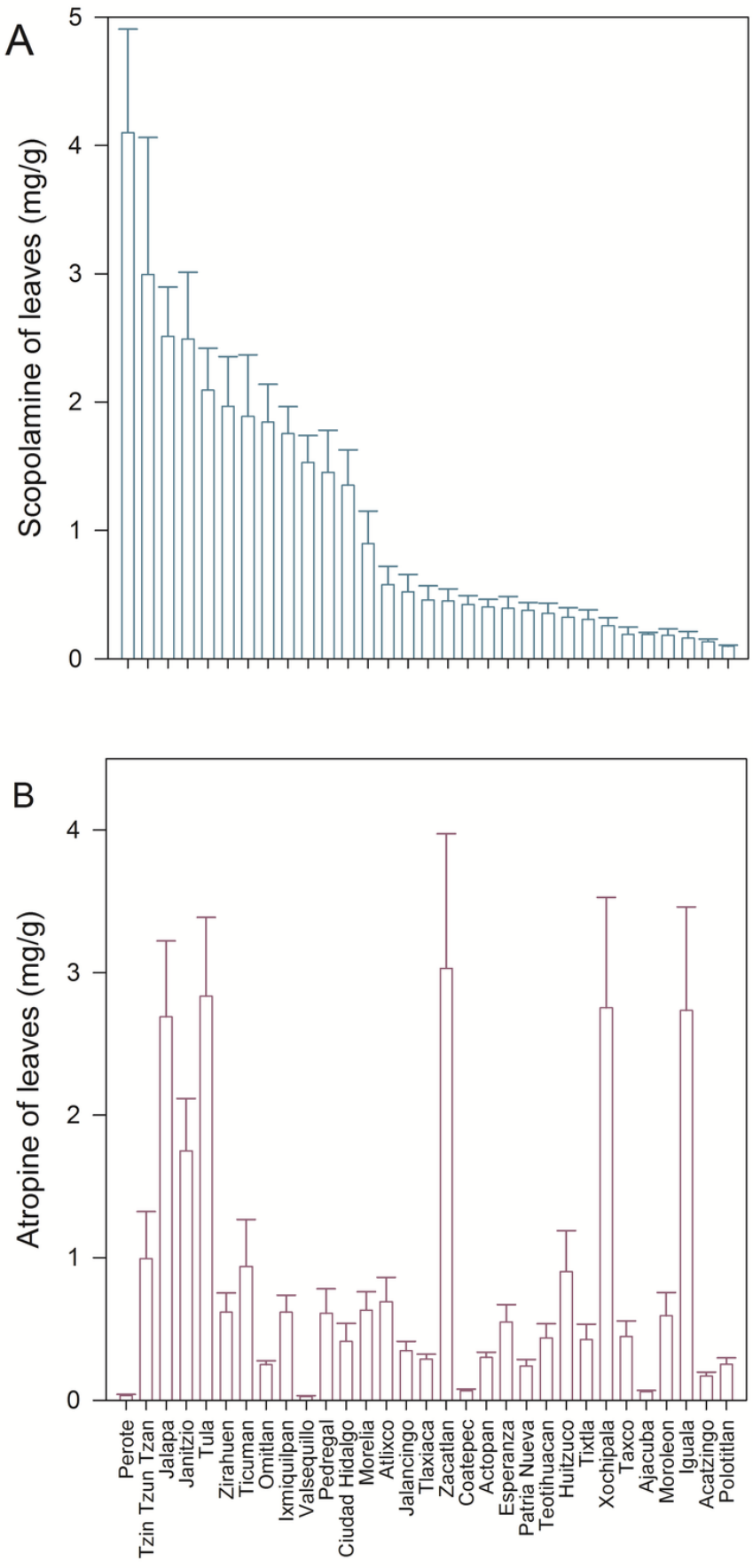
Datura stramonium populations sampled in Central Mexico. The number each population corresponds to the locality given in Table S1.



2

Figure 2

Average (+1 *S.E.*) concentration of scopolamine (A) and atropine in leaves (B), in 31 populations of *Datura stramonium* from central Mexico.


A
Scopolamine of leaves (mg/g)
0
1
2
3
4
5
B
Atropine of leaves (mg/g)
0
1
2
3
4
Perote
Tzin Tzun Tzan
Jalapa
Janitzio
Tula
Zirahuen
Ticuman
Omitlan
Ixmiquilpan
Valsequillo
Pedregal
Ciudad Hidalgo
Morelia
Atlixco
Jalancingo
Tlaxiaca
Zacatlan
Coatepec
Actopan
Esperanza
Patria Nueva
Teotihuacan
Huitzuco
Tixtla
Xochipala
Taxco
Ajacuba
Moroleon
Iguala
Acatzingo
Polotitlan
Populations

3

Figure 3

Average (+1 *S.E.*) concentration of scopolamine (A) and atropine (B) in seeds, in 14 populations of *Datura stramonium* from central Mexico.

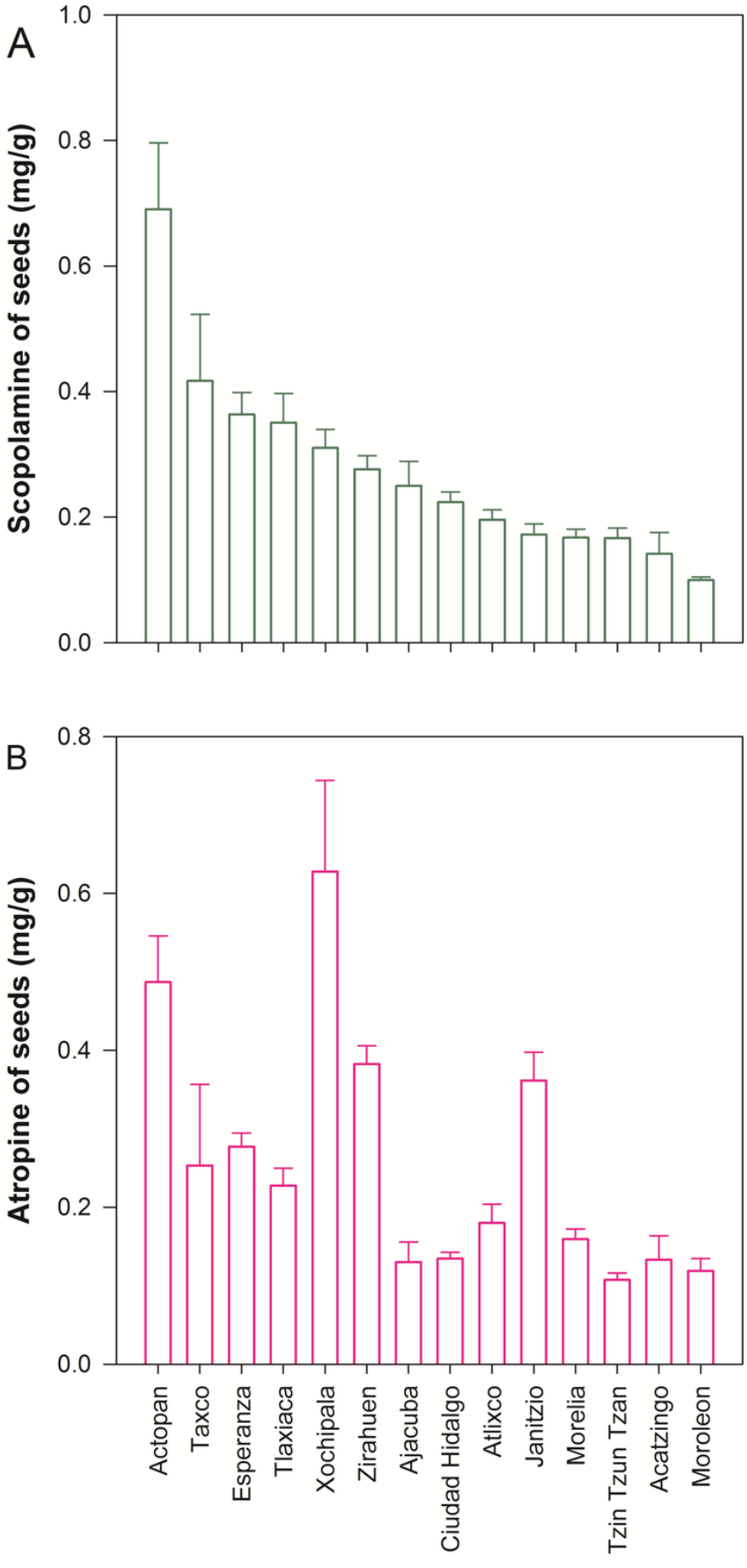

A
Scopolamine of seeds (mg/g)
1.0
0.8
0.6
0.4
0.2
0.0
B
Atropine of seeds (mg/g)
0.8
0.6
0.4
0.2
0.0
Actopan
Taxco
Esperanza
Tlaxiaca
Xochipala
Zirahuen
Ajacuba
Ciudad Hidalgo
Atlixco
Janitzio
Morelia
Tzin Tzun Tzan
Acatzingo
Moroleon
Populations

Table 1(on next page)

Table 1

Generalized linear models of the among population variation in the concentration of scopolamine and atropine in leaves and seeds, as well as the intensity of infestation (average number of weevils per fruit, per plant), and the proportion of infested fruits per plant in *Datura stramonium*.

Response variable	N	d.f.	Wald´s Chi-square	*P*	AICc
Scopolamine of leaves	278	31	684.55	< 0.0001	345.19
Atropine of leaves	278	31	875.11	< 0.0001	212.17
Scopolamine of seeds	119	14	13 441.13	< 0.0001	817.18
Atropine of seeds	119	14	13 062.42	< 0.0001	777.75
Intensity of infestation	859	28	835.98	< 0.0001	74.73
Proportion of infested fruits	859	28	1 562.36	< 0.0001	1 732.56

Notes

AICc, The corrected Akaike information criterion, gives a measure of the relative quality of a statistical model, considering the sample size.

4

Figure 4

Average (+1 *S.E.*) proportion of infested fruits per plant (A) and intensity of infestation (the total number of weevils divided by the total number of fruits per plant) (B) by *Trichobaris soror*, in 31 populations of *Datura stramonium* from central Mexico.

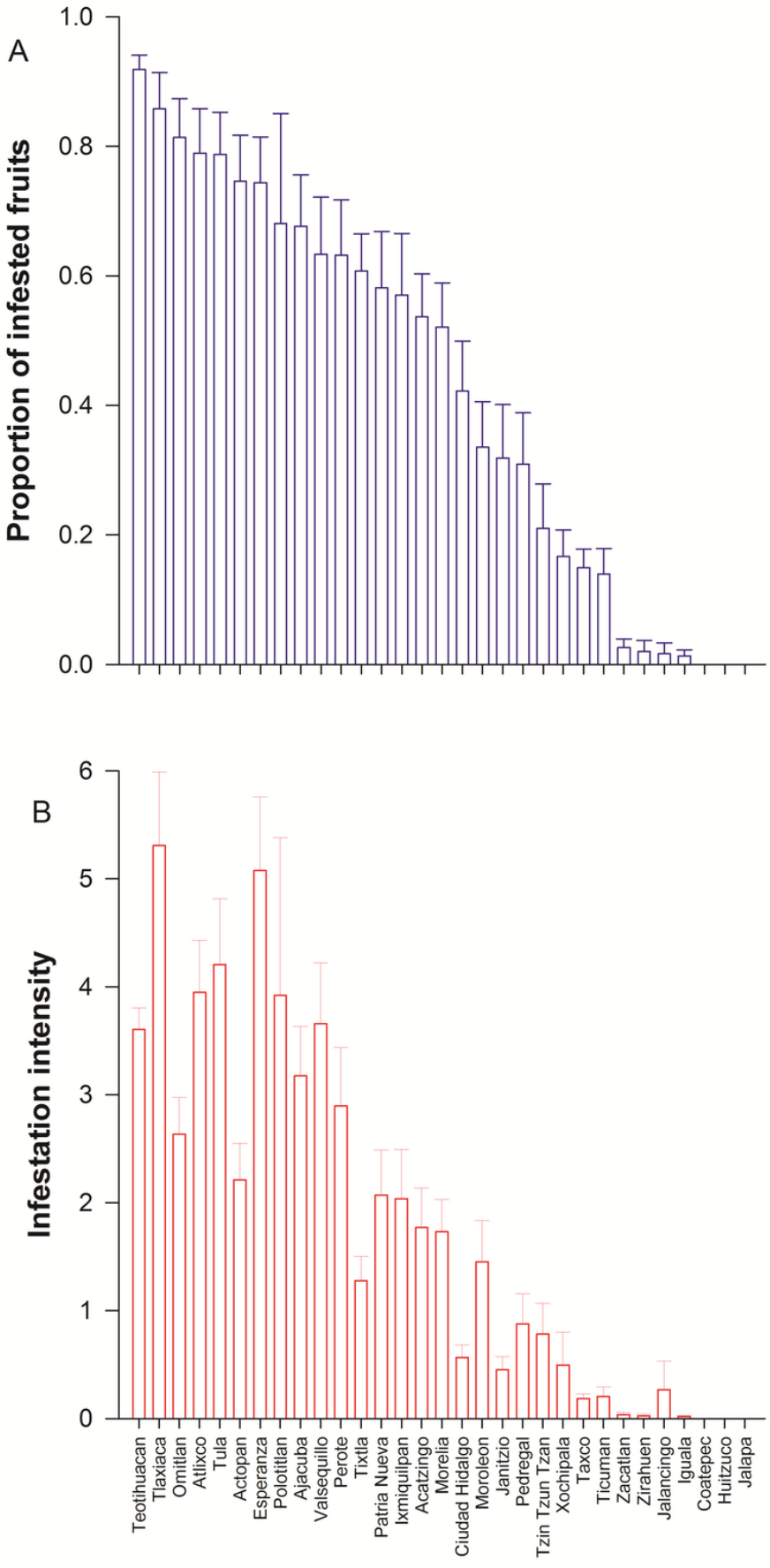

A
Proportion of infested fruits
1.0
0.8
0.6
0.4
0.2
0.0
B
Infestation intensity
6
5
4
3
2
1
0
Teotihuacan
Tlaxiaca
Omitlan
Atlixco
Tula
Actopan
Esperanza
Polotitlan
Ajacuba
Valsequillo
Perote
Tixtla
Patria Nueva
Ixmiquilpan
Acatzingo
Morelia
Ciudad Hidalgo
Moroleon
Janitzio
Pedregal
Tzin Tzun Tzan
Xochipala
Taxco
Ticuman
Zacatlan
Zirahuen
Jalancingo
Iguala
Coatepec
Huitzuco
Jalapa
Populations

Table 2(on next page)

Table 2

Generalized linear models of population average of the concentration of scopolamine and atropine in leaves and seeds of *Datura stramonium*, as a function of the selection differential (*S*) for the corresponding alkaloid, and environmental variables.

Response variable	Factors	N	d.f.	Wald´s Chi-square	*P*	AICc
Scopolamine of leaves	Lang´s aridity index	31	1	0.134	0.714	72.973
	Altitude		1	1.563	0.211	
	Latitude		1	0.552	0.458	
	Longitude		1	0.993	0.319	
	S Scopolamine		1	5.662	0.017	
Scopolamine of seeds	Lang´s aridity index	14	1	3.444	0.063	121.19
	Altitude		1	2.665	0.103	
	Latitude		1	0.579	0.447	
	Longitude		1	0.912	0.339	
	S Scopolamine		1	3.006	0.083	
Atropine of leaves	Lang´s aridity index	31	1	3.557	0.059	61.072
	Altitude		1	3.419	0.064	
	Latitude		1	0.004	0.95	
	Longitude		1	0.001	0.976	
	S Atropine		1	0.812	0.367	
Atropine of seeds	Lang´s aridity index	14	1	11.291	0.001	122.06
	Altitude		1	0.002	0.967	
	Latitude		1	1.666	0.197	
	Longitude		1	1.288	0.256	
	S Atropine		1	0.011	0.918	

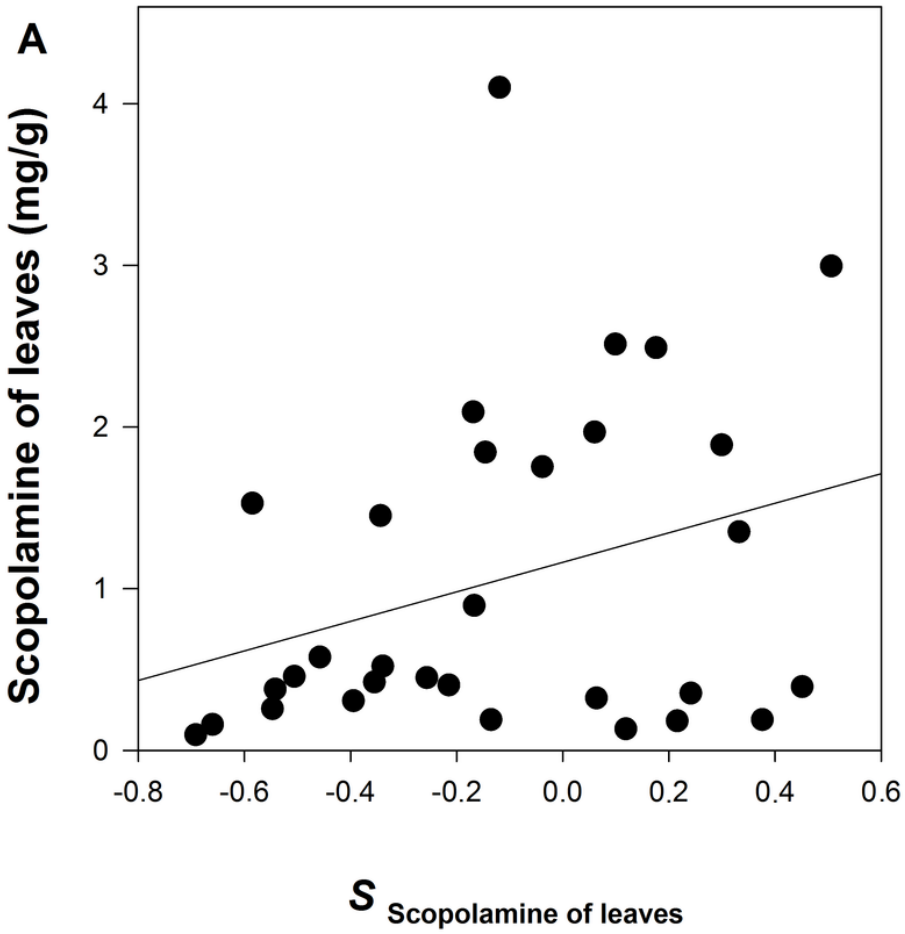
Notes

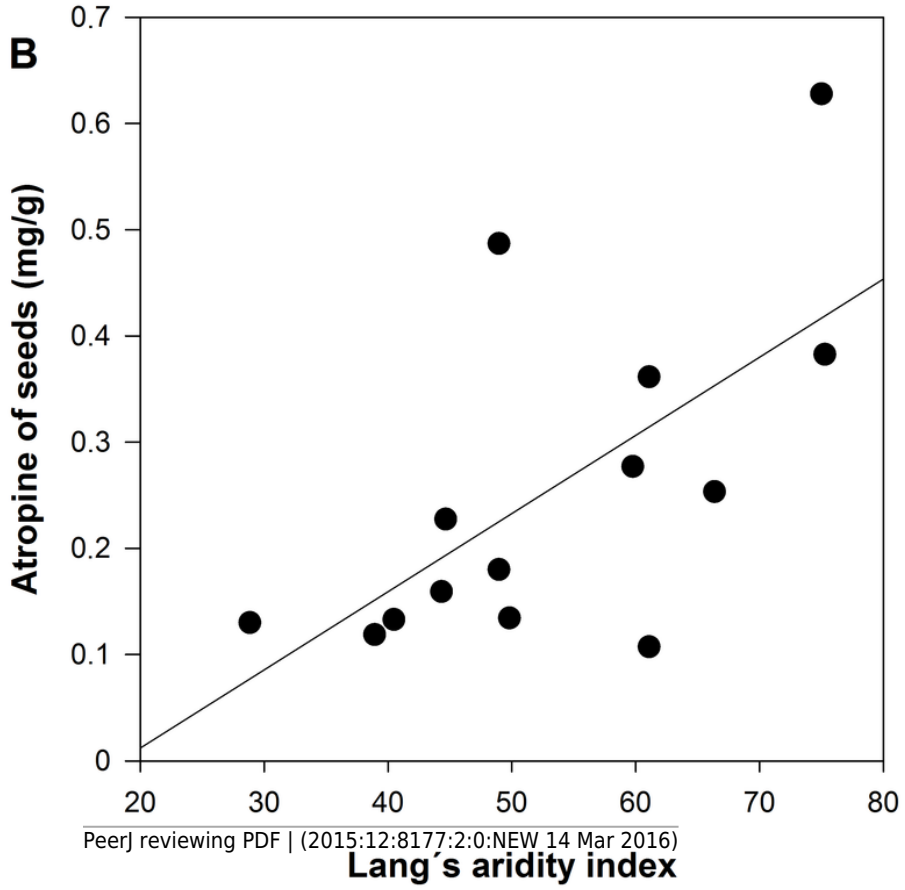
AICc, The corrected Akaike information criterion, gives a measure of the relative quality of a statistical model, considering the sample size.

5

Figure 5

Relationships between (A) the population average of scopolamine concentration in leaves with $S_{\text{Scopolamine of leaves}}$ (ρ = 0.3079), and (B) the population average of atropine concentrations in seeds with the Lang´s index (ρ = 0.6434).


A
Scopolamine of leaves (mg/g)
4
3
2
1
0
-0.8
-0.6
-0.4
-0.2
0.0
0.2
0.4
0.6
S Scopolamine of leaves


B
Atropine of seeds (mg/g)
0.7
0.6
0.5
0.4
0.3
0.2
0.1
0
20
30
40
50
60
70
80
Lang´s aridity index