Natural enemy release or biotic resistance? Insect herbivores associated with the exotic *Solanum viarum* (Solanaceae) and a sympatric native congener in KwaZulu-Natal, South Africa

Terence Olckers, Kwanele Msele and Daniella Egli

School of Life Sciences, University of KwaZulu-Natal, Scottsville, South Africa.

Native to South America, *Solanum viarum* Dunal (tropical soda apple; Solanaceae) is naturalised in several countries globally. The plant is a major invader in the southern USA, but has minor weed status in South Africa. We investigated whether *S. viarum* has escaped natural enemy pressure or has recruited insect herbivores from the local *Solanum* flora, which are exerting some level of biotic resistance. Insect species richness and abundance and the resulting levels of herbivory were compared between plants from sympatric populations of *S. viarum* and the native *Solanum dasyphyllum* Schumacher and Thonning in the KwaZulu-Natal Midlands. Foliage, floral material, and fruits were collected across seasons from 20 plants of each species and assessed in the laboratory. Despite no significant differences between the two species in the size of the sampled plants, *S. viarum* displayed significantly lower insect herbivore diversity and abundance and suffered significantly lower levels of damage to its photosynthetic and reproductive tissues. Five of the 11 specialist herbivore species recorded on *S. dasyphyllum* were associated with *S. viarum*, but in substantially lower numbers and in fewer samples. The flowerbud-galling moth *Scrobipalpa* sp. (Gelechiidae), which prevents fruiting in *S. dasyphyllum*, was absent on *S. viarum* and indicative of the negligible floral damage on *S. viarum*. Although the fruit of *S. viarum* were occasionally utilised by specialist herbivores, seed damage was similarly negligible. Due to its release from specialist natural enemies and with no evidence of biotic resistance, *S. viarum* may increase in weed status in South Africa.

INTRODUCTION

Solanum viarum Dunal (Solanaceae), commonly known as tropical soda apple, is a prickly shrub that is native to northern Argentina, southern Brazil, Uruguay and Paraguay (Mullahey et al. 1993; Olckers et al. 2002; Welman 2003). The plant is naturalised in several countries including Australia, China, India, Mexico, the United States of America, the West Indies, and South Africa (Coile 1993; Welman 2003; Diaz et al. 2014). *Solanum viarum* bears broad sticky leaves due to glandular trichomes, numerous thorns, distinctive yellow fruits, and cream-coloured flowers (Coile 1993; Mullahey et al. 1993). Individual plants can produce in excess of 50 000 seeds annually, which are dispersed by cattle, wild animals, contaminated agricultural produce and machinery, and humans (Coile 1993; Mullahey et al. 1993). The unpalatability of its foliage for browsing animals contributes largely to the plant's competitive advantage (Mullahey et al. 1993). *Solanum viarum* became a major invasive weed of pastures, conservation areas and disturbed habitats in the southern states of the USA, leading to the implementation of a successful biological control programme (Diaz et al. 2014).

The Enemy Release Hypothesis (Keane and Crawley 2002) proposes that invasive exotic plants gain a competitive advantage over native flora, due to escape from their co-evolved natural enemies outside of their natural habitats. This phenomenon can interact with other factors, including resource availability, lack of biotic resistance, and disturbance, to enhance the success of invasion by exotic plants in their new habitats (Blumenthal 2006; Maron and Vilá 2001; Jeschke 2014). Although widely distributed in the Eastern Cape and KwaZulu-Natal provinces of South Africa, and neighbouring Swaziland (Welman 2003), *S. viarum* is currently regarded as a weed of minor importance (Welman 2003; Henderson 2020). One possible explanation for the plant's low weed status in South Africa is that it has attracted specialist insect herbivores from native plants in the genus *Solanum* (Olckers and Hulley 1989a, b, 1991) and/or generalist herbivores, thereby substituting for natural enemy release and subjecting it to some degree of natural control. This scenario would conform to the Biotic Resistance Hypothesis (see Maron and Vilá 2001; Jeschke 2014).

The aim of this study was to determine whether *S. viarum* has recruited specialist insect herbivores from related congeneric plants or has remained relatively free of insect attack. This was achieved by comparing the insect herbivore faunas and the levels of damage inflicted on the foliage, flowers and fruit of *S. viarum* versus the native congener *Solanum dasyphyllum* Schumacher and Thonning (previously called *S.* cf. *acanthoideum* E. Meyer in Olckers and Hulley (1991)). These two species are similar in size and architecture and typically co-occur in the same habitats in the Midlands region of KwaZulu-Natal, where *S. viarum* was first recorded (Welman 2003). Low insect herbivore species richness and abundance, compounded by a lack of specialist species, and consequently low levels of damage on *S. viarum* relative to *S. dasyphyllum* would indicate natural enemy release (e.g. DeWalt et al. 2004). In contrast, equivalent insect herbivore faunas and levels of damage on the two *Solanum* species would indicate biotic resistance through natural enemy substitution and explain the limited invasiveness of *S. viarum* recorded at present.

MATERIALS AND METHODS

Study sites

Individual plants of *S. viarum* and *S. dasyphyllum* were sampled at six localities around Pietermaritzburg, KwaZulu-Natal province, South Africa where populations of both species occur in sympatry (Table 1). Twenty plants of each species were sampled on nine occasions during 2023/24. Voucher specimens of both species were lodged in the University of KwaZulu-Natal John Bews Herbarium (NU).

Sampling protocol

On each sampling occasion, equal numbers of plants of both species were sampled, with various components (foliage, fruits, and flowers) collected for later analysis. The height of each plant was measured prior to sampling. A branch that included the top 30 cm of foliage was removed from each plant, placed in a paper bag, and stored in a freezer for later assessment. When present, additional floral tissues (flowers and buds) and fruit were collected from each plant and placed in emergence containers in the laboratory to rear immature insect stages to adulthood. The leaves from the frozen material were inspected under a dissecting microscope to record ectophagous insects, while the stems, fruits, and floral material were dissected to record endophagous immature stages. Floral and fruit material in the emergence containers were dissected after 2–3 weeks and 6–8 weeks, respectively, to record any remaining immature stages.

All collected insects, including herbivores, predators and parasitoids, were preserved in 70% alcohol or pinned for later comparisons and the numbers of individuals of each insect species were recorded for each sampled plant. Species where single individuals were recorded only once were excluded. Specialist herbivore taxa were regarded as those typically associated with native *Solanum* species in South Africa (see Olckers and Hulley 1989a, b, 1991; Olckers et al. 1995).

Assessments of insect damage were made during the processing of the different plant tissues. Leaf damage on each sampled plant was scored on a scale from 0 to 3, which ranged from no clear damage (0), very little damage (1), moderate damage (2) to considerable damage (3). Floral and fruit damage for each sampled plant was recorded as the percentages of flowerbuds/flowers and fruit (from both the frozen samples and emergence containers) that were infested by insects.

Statistical analysis

The data were analysed using IBM SPSS version 29. Since the data did not meet the assumptions of normality or equality of variances, non-parametric tests and generalised linear models were used to determine statistical significance ($p < 0.05$). Plant height, insect species richness, insect abundance, and leaf damage scores were compared between the two *Solanum* species using independent-samples median tests (Yates's continuity corrected). The proportions of insect-infested versus uninfested floral material and fruit were compared between the two plant species using models that incorporated a binomial distribution and a logit-link function. These models were corrected for over-dispersion by means of scale weight variables and significance ($p < 0.05$) was determined using Wald chi-square statistics.

RESULTS

Insect species richness and abundance

Nineteen insect species (15 herbivorous) were recorded on *S. viarum*, compared to 33 species (26 herbivorous) on *S. dasyphyllum*. Consequently, there was significantly lower median insect species richness, which included all recorded species ($\chi^2 = 5.385$, df = 1, $p = 0.02$) and herbivorous species ($\chi^2 = 14.731$, df = 1, $p < 0.001$) on *S. viarum* (Figure 1). Similarly, there was significantly lower median insect abundance on *S. viarum* in relation to all recorded insects ($\chi^2 = 10.025$, df = 1, $p = 0.002$) and herbivorous insects ($\chi^2 = 16.900$, df = 1, $p < 0.001$) (Figure 2). There was no significant difference in median plant height between *S. viarum* and *S. dasyphyllum* ($\chi^2 = 0.100$, df = 1, $p = 0.752$), suggesting that plant size did not influence insect species richness or abundance.

Insect herbivore composition

The insect herbivore fauna associated with *S. viarum* was largely comprised of generalist species that were present in a low proportion of samples. Only five species, which included one foliage feeder, one flower feeder and three fruit feeders, were regarded as specialists that are typically associated with native *Solanum* species, but none were recorded in more than 30% of the samples (Table 2). In contrast, the insect herbivore fauna associated with *S. dasyphyllum* included 11 specialists, comprising four foliage feeders, two flower feeders and five fruit feeders, with seven species recorded in more than 30% of the samples (Table 2). When present on both species, the incidence (i.e. presence in samples) and mean abundance of these specialist species was substantially higher on *S. dasyphyllum* (Table 2).

Levels of insect damage

On average, very low leaf damage scores (mean ± SE = 1.0 ± 0.1) were recorded on *S. viarum* and were significantly lower ($\chi^2 = 22.727$, df = 1, $p < 0.001$) than the moderate scores (2.3 ± 0.2) recorded on *S. dasyphyllum*. Most leaf damage on *S. dasyphyllum* was attributed to adults and larvae of the herbivorous ladybird *Epilachna hirta* (Coccinellidae) and adults of the flea beetle *Chaetocnema* sp. (Chrysomelidae), which were recorded in ≥50% of foliar samples (Table 2).

Table 1: Localities around Pietermaritzburg, KwaZulu-Natal where individual plants of *Solanum viarum* and *Solanum dasyphyllum* were sampled.

Date	Locality, habitat	Coordinates	Altitude	No. plants
08/03/2023	Cedara farm, paddock	29°32'22' S, 30°16'05'' E	1068	2 of each species
22/03/2023	Ashburton, disturbed rangeland	29°41'37'' S, 30°29'54'' E	770	3 of each species
29/03/2023	Ukulinga farm, paddock	29°39'42'' S, 30°24'14'' E	780	2 of each species
19/04/2023	Ashburton, disturbed rangeland	29°41'37'' S, 30°29'54'' E	770	2 of each species
30/08/2023	Ukulinga farm, research plots	29°40'13'' S, 30°24'03'' E	840	3 of each species
26/09/2023	Lion Park road, disturbed rangeland	29°39'51'' S, 30°31'26'' E	750	1 of each species
15/11/2023	Lion Park road, disturbed rangeland	29°39'51'' S, 30°31'26'' E	750	2 of each species
19/03/2024	Ashburton, disturbed rangeland	29°41'37'' S, 30°29'54'' E	770	3 of each species
24/03/2024	Ashburton, disturbed rangeland	29°41'37'' S, 30°29'54'' E	770	2 of each species

Table 2: Incidence[1] and abundance[2] of specialist insect herbivories associated with *Solanum viarum* and *Solanum dasyphyllum*.

Insect herbivore species	S. viarum		S. dasyphyllum	
	Incidence	Number	Incidence	Number
Foliage				
Unidentified leaf hopper (Cicadellidae)	–	–	90	5.3 ± 1.6
Epilachna hirta (Thunberg) (Coccinellidae)	5	0.1 ± 0.1	55	1.4 ± 0.4
Chaetocnema sp. (Chrysomelidae)	–	–	50	1.7 ± 0.6
Conchyloctenia hybrida (Boheman) (Chrysomelidae)	–	–	10	0.1 ± 0.1
Flowers				
Scrobipalpa sp. nr. *concreta* (Meyrick) (Gelechiidae)	-	-	78	3.3 ± 0.7
Pria sp. (Nitidulidae)	25	1.2 ± 0.6	44	4.5 ± 1.6
Fruit				
Daraba laisalis (Walker) (Pyraustidae)	30	2.7 ± 1.3	78	6.9 ± 1.9
Silba ophyroides (Bezzi) (Lonchaeidae)	20	4.4 ± 2.8	56	6.5 ± 2.2
Unidentified fly 1 (Agromyzidae)	10	0.2 ± 0.2	17	2.2 ± 1.3
Unidentified fly 2 (Agromyzidae)	–	–	28	3.4 ± 1.9
Unidentified fly 3 (Agromyzidae)	–	–	6	0.2 ± 0.2

[1]Percentage of sampled plants on which each insect species was present.
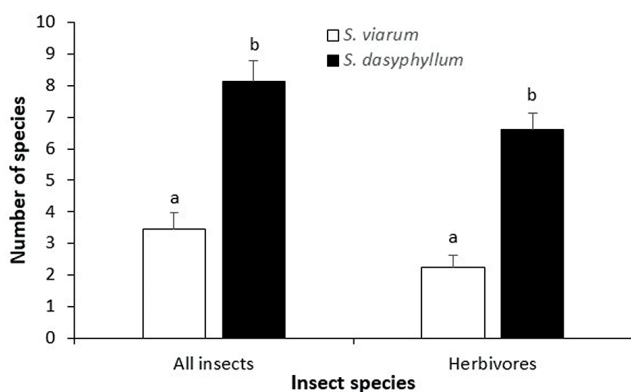[2]Mean (± SE) number of insects per sampled plant.

Figure 1: Mean (+ SE) number of insect species (all species and herbivores only) recorded on *Solanum viarum* and *Solanum dasyphyllum*. Different letters above the bars indicate significant differences.
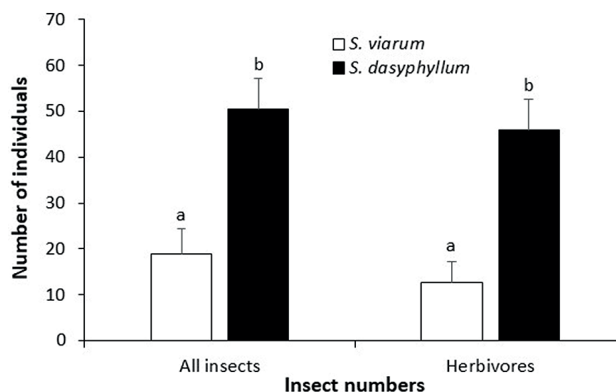

Figure 2: Mean (+ SE) number of insect individuals (all species and herbivores only) recorded on *Solanum viarum* and *Solanum dasyphyllum*. Different letters above the bars indicate significant differences.

The percentage of floral material infested by endophagous insects (Figure 3) was also significantly lower (χ^2 = 12.218, df = 1, $p < 0.001$) on *S. viarum* (mean ± SE = 3.0 ± 1.7%) than on *S. dasyphyllum* (48.1 ± 8.7%). The flower-boring beetle *Pria* sp. (Nitidulidae) was recorded on both species, albeit less frequently and abundantly on *S. viarum* (Table 2). In contrast, the flower-galling moth *Scrobipalpa* sp. (Gelechiidae), which prevents fruit formation by *S. dasyphyllum*, was absent on *S. viarum* but present in 78% of floral samples collected from *S. dasyphyllum* (Table 2). On average, 41.6% (± 9.3%) of the floral components sampled on *S. dasyphyllum* plants comprised galled buds, accounting for the major difference in floral damage between the two *Solanum* species.

Similarly, the percentage of fruit infested by endophagous insects (Figure 3) was significantly lower (χ^2 = 9.708, df = 1, p = 0.002) on *S. viarum* (mean ± SE = 11.5 ± 4.1%) than on *S. dasyphyllum* (49.2 ± 9.0%). Although the fruit-boring moth *D. laisalis* (Pyraustidae) and two fruit-feeding flies, *S. ophyroides* (Lonchaeidae) and an unidentified species of Agromyzidae, were recorded on both *Solanum* species, they were more frequent and abundant on *S. dasyphyllum* (Table 2). In any event, the impact of these fruit borers was negligible, with *D. laisalis* caterpillars damaging few seeds within infested fruits.
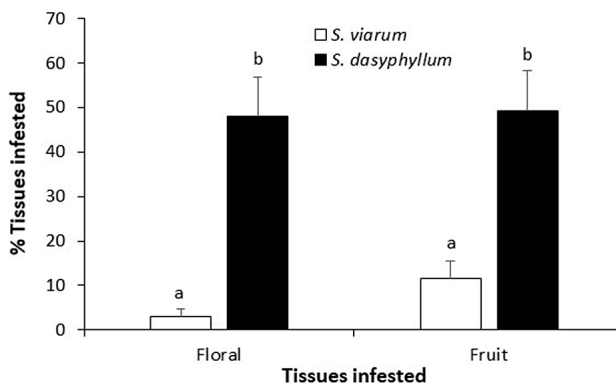

Figure 3: Mean (+ SE) percentage of floral tissues and fruit of *Solanum viarum* and *Solanum dasyphyllum* plants infested by endophagous insect larvae. Different letters above the bars indicate significant differences.

DISCUSSION

Solanum viarum has been present in South Africa for more than 60 years, with the first recorded specimen collected around Pietermaritzburg, KwaZulu-Natal in 1962 (Welman 2003).

However, the plant was not recognised by Arnold and De Wet (1993) in their list of Solanaceae present in South Africa and its identity was only confirmed later (see Welman 2003). The plant has previously been misidentified and confused with both exotic (e.g. *S. aculeatissimum* Jacquin) and native (e.g. *S. acanthoideum* E. Meyer and *S. panduriforme* E. Meyer) congeners in South Africa (Olckers et al. 1995; Hill et al. 1997; Welman 2003). In South Africa, *S. viarum* has low weed status (Welman 2003) relative to other exotic congeners, notably *S. elaeagnifolium* Cavanilles, *S. mauritianum* Scopoli and *S. sisymbriifolium* Lamarck, and is currently not listed under the South African alien plant legislation (Henderson 2020). Since the plant has been brought under biological control in the USA, following the introduction of the tortoise beetle *Gratiana boliviana* Spaeth (Chrysomelidae), we considered whether recruited native specialists were having a similar impact in South Africa. In particular, the insect faunas of native *Solanum* species are largely comprised of oligophagous species that utilise several congeneric host-plant species (see Olckers and Hulley 1989a, b, 1991, 1995; Olckers et al. 1995) and could thus have included *S. viarum* in their host range.

However, our study revealed that *S. viarum* has remained largely free of natural enemy pressure, with significantly lower insect herbivore richness, abundance, specialist composition, and damage levels relative to the native *S. dasyphyllum*. These trends were previously reported in South Africa for the exotic *S. elaeagnifolium* (Hill et al. 1993; Olckers and Hulley 1995), *S. mauritianum* (Olckers and Hulley 1989a, 1991, 1995) and *S. sisymbriifolium* (Hill et al. 1993; Olckers and Hulley 1995). Although *S. viarum* and *S. dasyphyllum* belong to the subgenus *Leptostemonum* Bitter, *S. viarum* falls under the Section *Acanthophora* Dunal, which is not native to southern Africa (Welman 2003; Vorontsova et al. 2013). In addition, Hill et al. (1997) reported two types of glandular trichomes on the leaves of *S. viarum* (misidentified as *S. acanthoideum*), which are renowned as anti-herbivore defences and are not typical of *S. dasyphyllum* leaves. Indeed, glandular trichomes on the leaves of *S. sisymbriifolium* significantly reduced the feeding and survival of the native *Solanum*-feeding tortoise beetle *Conchyloctenia tigrina* Olivier (Chrysomelidae), but not the South American tortoise beetle *Gratiana spadicea* (Klug) that utilises this plant as a host, thereby explaining the poor insect herbivore fauna associated with the plant in South Africa (Hill et al. 1993).

Beside glandular trichomes, the chemical defences of *S. viarum* may also prohibit its utilisation by native solanaceous insects. High concentrations of secondary metabolites, notably phenolic compounds and acylsugars, together with leaf trichomes, deterred feeding and survival of the polyphagous agricultural pest *Helicoverpa armigera* (Hübner) (Lepidoptera: Noctuidae), advocating the use of *S. viarum* as a trap plant in croplands (Gyawali et al. 2022). These considerations, evidenced by the absence of specialists like the flowerbud-galling moth *Scrobipalpa* sp. that reduces fruiting in several native *Solanum* species (Olckers and Hulley 1989b, 1991), suggest that *S. viarum* could increase its weed status in South Africa. In particular, despite the unpalatability of the plant's foliage, its ripe yellow fruit are ingested by cattle and wild animals, which facilitated its rapid distribution in the USA (Mullahey et al. 1993; Diaz et al. 2014).

Since *S. viarum* has a low weed status in South Africa, the Enemy Release Hypothesis (Keane and Crawley 2002), which predicts the opposite, does not explain the plant's population status. Rather, *S. viarum* is a minor weed despite exhibiting release from specialist natural enemies. However, we acknowledge that the study did not consider the role of plant pathogens as specialist natural enemies in this context. Although there are several examples of biotic resistance, where exotic plants have recruited diverse assemblages of native herbivores that have reduced their invasive properties (Maron and Vilá 2001), this study produced no evidence for the Biotic Resistance Hypothesis (Jeschke 2014).

While other biotic factors may be limiting its invasion potential (e.g. resistance from native flora), *S. viarum* may still be in the early stages of invasion and increase its weed status in the future. Should this occur, biological control using the defoliating beetle *G. boliviana* (Diaz et al. 2014) should be considered, since neither native solanaceous specialists nor generalist species are contributing to the plant's control.

AUTHOR CONTRIBUTIONS

TO: conceptualisation; project administration; investigation; data curation; formal analysis; supervision; writing – original draft.
KM: investigation; data curation; formal analysis; writing – review and editing.
DE: investigation; supervision; writing – review and editing.

ORCID IDS

Terence Olckers: https://orcid.org/0000-0001-6750-8683
Kwanele Msele: https://orcid.org/0000-0003-2030-8224
Daniella Egli: https://orcid.org/0000-0002-6922-7970

REFERENCES

Arnold TH, De Wet BC. 1993. Plants of Southern Africa: Names and Distribution. Memoirs of the Botanical Survey of South Africa, Vol. 62. National Botanical Institute, Pretoria, South Africa. 825 p.

Blumenthal DM. 2006. Interactions between resource availability and enemy release in plant invasion. Ecology Letters 9(7): 887–895. https://doi.org/10.1111/j.1461-0248.2006.00934.x.

Coile NC. 1993. Tropical soda apple, *Solanum viarum* Dunal: The plant from hell (Solanaceae). Florida Division of Plant Industry, Department of Agriculture and Consumer Affairs, Botany Circular 27: 1–4.

DeWalt SJ, Denslow JS, Ickes K. 2004. Natural-enemy release facilitates habitat expansion of the invasive tropical shrub *Clidemia hirta*. Ecology 85(2): 471–483. https://doi.org/10.1890/02-0728.

Diaz R, Manrique V, Hibbard K, Fox A, Roda A, Gandolfo D, McKay F, Medal J, Hight S, Overholt WA. 2014. Successful biological control of tropical soda apple (Solanales: Solanaceae) in Florida: A review of key program components. Florida Entomologist 97(1): 179–190. https://doi.org/10.1653/024.097.0124.

Gyawali P, Hwang S-Y, Sotelo-Cardona P, Srinivasan R. 2022. Elucidating the fitness of a dead-end trap crop strategy against the tomato fruitworm, *Helicoverpa armigera*. Insects 2021, 12(6): 506. https://doi.org/10.3390/insects12060506.

Henderson L. 2020. Invasive alien plants in South Africa. Plant Protection Research Institute Handbook No. 21. Agricultural Research Council, South Africa. 384 p.

Hill MP, Hulley PE, Olckers T. 1993. Insect herbivores on the exotic weeds *Solanum elaeagnifolium* Cavanilles and *S. sisymbriifolium* Lamarck (Solanaceae) in South Africa. African Entomology 1(2): 175–182.

Hill MP, Hulley PE, Allsopp J, van Harmelen G. 1997. Glandular trichomes on the exotic *Solanum sisymbriifolium* Lamarck (Solanaceae): Effective deterrents against an indigenous South African herbivore. African Entomology 5(1): 41–50.

Jeschke JM. 2014. General hypotheses in invasion ecology. Diversity and Distributions 20(11): 1229–1234. https://doi.org/10.1111/ddi.12258.

Keane RM, Crawley MJ. 2002. Exotic plant invasions and the enemy release hypothesis. Trends in Ecology and Evolution 17(4): 164–170. https://doi.org/10.1016/S0169-5347(02)02499-0.

Maron JL, Vilà M. 2001. When do herbivores affect plant invasion? Evidence for the natural enemies and biotic resistance hypotheses. Oikos 95: 361–373. https://doi.org/10.1034/j.1600-0706.2001.950301.x.

Mullahey JJ, Nee M, Wunderlin RP, Delaney KR. 1993. Tropical soda apple (*Solanum viarum*): A new weed threat in subtropical

regions. Weed Technology 7(3): 783–786. https://doi.org/10.1017/S0890037X00037714.

Olckers T, Hulley PE. 1989a. Insect herbivore diversity on the exotic weed *Solanum mauritianum* Scop. and three other *Solanum* species in the eastern Cape Province. Journal of the Entomological Society of Southern Africa 52(1): 81–93.

Olckers T, Hulley PE. 1989b. Seasonality and biology of common insect herbivores attacking *Solanum* plants in the eastern Cape Province. Journal of the Entomological Society of Southern Africa 52(1): 109–118.

Olckers T, Hulley PE. 1991. Impoverished insect herbivore faunas on the exotic bugweed *Solanum mauritianum* Scop. relative to indigenous *Solanum* species in Natal/KwaZulu and the Transkei. Journal of the Entomological Society of Southern Africa 54(1): 39–50.

Olckers T, Hulley PE. 1995. Importance of preintroduction surveys in the biological control of *Solanum* weeds in South Africa. Agriculture, Ecosystems & Environment 52(2-3): 179–185. https://doi.org/10.1016/0167-8809(94)00537-O.

Olckers T, Hulley PE, Hill MP. 1995. Insect herbivores associated with indigenous species of *Solanum* (Solanaceae) in the Transvaal, South Africa, and in Namibia. African Entomology 3(1): 49–57.

Olckers T, Medal JC, Gandolfo DE. 2002. Insect herbivores associated with species of *Solanum* (Solanaceae) in northeastern Argentina and southeastern Paraguay, with reference to biological control of weeds in South Africa and the United States of America. Florida Entomologist 85(1): 254–260. https://doi.org/10.1653/0015-4040(2002)085[0254:IHAWSO]2.0.CO;2.

Vorontsova MS, Stern S, Bohs L, Knapp S. 2013. African spiny *Solanum* (subgenus *Leptostemonum*, Solanaceae): A thorny phylogenetic tangle. Botanical Journal of the Linnean Society 173(2): 176–193. https://doi.org/10.1111/boj.12053.

Welman WG. 2003. The genus *Solanum* (Solanaceae) in southern Africa; subgenus *Leptostemonum*, the introduced sections *Acanthophora* and *Torva*. Bothalia 33(1): 1–18. https://doi.org/10.4102/abc.v33i1.429.