PLANT SIGNALING & BEHAVIOR
2021, VOL. 16, NO. 11, e1964163 (6 pages)
https://doi.org/10.1080/15592324.2021.1964163

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SHORT COMMUNICATION

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Exploring the role of soil types on defense and fitness traits of silverleaf nightshade (*Solanum elaeagnifolium*), a worldwide invasive species through a field survey in the native range

Stephanie Kasper[a], Jesus Chavana[a], Lekshmi Sasidharan[b], Alexis Racelis[c], and Rupesh Kariyat[a]

[a]Department Of Biology, University Of Texas Rio Grande Valley, Edinburg, TX, USA; [b]School Of Mathematical And Statistical Sciences, University Of Texas Rio Grande Valley, Edinburg, Tx, USA; [c]School Of Earth, Environment And Marine Sciences, University Of Texas Rio Grande Valley, Edinburg, TX, USA

ABSTRACT

Silverleaf nightshade (*Solanum elaeagnifolium*) is a highly successful invasive weed that has caused agricultural losses both in its home and invaded ranges. Surveying 50 sub-populations over 36,000 km^2 in its native range in South Texas, we investigated the interactions among soil type, population size, plant height, herbivory, and plant defenses in its home range with the expectation that populations growing in the plant's preferred sandier soils would host larger colonies of healthier and better defended plants. At each sampling location, on randomly selected plants, we measured height, insect herbivore damage, and presence, and density of internode spines. Soil type was determined using the NRCS Web Soil Survey and primarily grouped into sand, clay, or urban. Our results show a tradeoff between growth and defense with larger colonies and taller plants in clay soils, but smaller colonies of shorter, spinier plants in sandy soils. We also observed decreased herbivory in urban soils, further confirming the plant's ability to survive and even be strengthened by highly disturbed conditions. This study is a starting point for a better understanding of silverleaf nightshade's ecology in its home range and complicates the assumption that it thrives best in sandy soils.

ARTICLE HISTORY
Received 10 July 2021
Revised 30 July 2021
Accepted 1 August 2021

KEYWORDS
Clay; herbivory; spines; fitness; invasion

Introduction

Through human migration, travel, and trade, an estimated 500,000 species have been transported outside their home territories and spread around the world.[1] Many of those species have become invasive, and their uncontrolled expansion beyond their ancestral range has caused economic and ecological harm.[2] Invasive plants displace native plant species, disrupt food webs, modify fire patterns, reduce agricultural and native plant productivity, and damage pastures, and consequently, their grazing quality.[3] The global economic impact of invasive species and efforts to control them has not been well assessed[4] but is estimated to cause $120 billion in annual damages just for the United States.[1]

Silverleaf nightshade (*Solanum elaeagnifolium*; Solanaceae; SLN) is a highly successful invasive weed that has caused agricultural losses both in its home range in the southwestern United States and northern Mexico, and globally, invading areas including Australia, South Africa, Morocco, Israel, and Greece.[5–7] Most invasive plants are better studied in the regions they invade than in their ancestral territories, an imbalance that makes patterns among successful invaders more difficult to detect.[8] SLN follows this pattern and has been widely studied in Australia, South Africa, and the Mediterranean where it is a new or expanding threat[9–11] but less frequently assessed in its home territory in Texas and northern Mexico.[12,13]

Insect surveys for potential biocontrol agents have been conducted in Mexico and Texas and studies have assessed the suitability of biocontrol candidates for introduction,[10,14,15] but many knowledge gaps remain unaddressed, regarding the ecology of SLN in its ancestral range. We recently showed that continuous mowing in this species can enhance defense and fitness traits with spillover effects into the next generation in the form of enhanced germination and reduced herbivory in lab and field.[16] SLN's deep roots, hardiness under arid conditions, potential toxicity to livestock, easy spread through seeds, rhizomes, and root fragments, and resistance to herbicides and mechanical control combine to make it a challenging and expensive weed to control once established [17, 18, Figure 1a-D].

In addition to the above said traits, SLN is a strong invader due to its suite of physical and chemical defenses against herbivory. The leaves and stem are covered in radial, non-glandular stellate trichomes and prickly spines that can injure animals and reduce herbivory.[19–22] As an added deterrent to herbivory, SLN also produces toxic secondary metabolites including alkaloids, tannins, and terpenes at levels that can repel insect herbivores and induce moderate poisoning symptoms in cattle and horses.[18,23]

CONTACT Rupesh Kariyat rupesh.kariyat@utrgv.edu Department Of Biology, University Of Texas Rio Grande Valley, Edinburg, Tx, USA
#These authors contributed equally to this work.
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Figure 1. Growth pattern and herbivory in silver-leaf nightshade, *Solanum elaeagnifolium*. (a) plants before flowering, (b) mature fruits, (c) leaf damage, and (d) flower damage.

In its native range, a variety of insect herbivores including Texas potato beetle (*Leptinotarsa texana*; Chrysomelidae; Coleoptera), lacebug (*Gargaphia arizonica*; Tingidae; Hemiptera), twirler moth (*Frumenta nephelomicta*; Gelechiidae; Lepidoptera), and tobacco hornworm (*Manduca sexta*; Sphindidae; Lepidoptera) have adapted to the plant's defenses and keep SLN under check.[9,12,22,24] Texas potato beetle has been evaluated for introduction as a biocontrol agent in Australia and already introduced in South Africa where native insects avoid the well-defended nightshade, and the species thrives without herbivore pressure.[10,25]

The quality and intensity of defenses varies widely across populations of *S. elaeagnifolium* due to herbivory intensity, insect pressure, plant health, and other soil and climatic conditions.[12,16] Soil properties like texture and pH can strongly influence both the composition of weed communities and the characteristics of individuals within those communities.[26] Surveys conducted in Australia suggest that SLN thrives best in coarse-textured sandy soil.[7,17,18] A preference for sandy soil has also been observed in Greece[27] though it has been suggested that other soil types may do little to deter plant establishment.[5] However, little is known about the plant's soil-type preferences in south Texas and how soil conditions relate to plant vigor and defenses. Clearly, a better understanding of the understudied relationship between SLN and soil conditions may allow for more targeted and efficient control tactics in both its home and invasive ranges,

Soils of south Texas, the native range of SLN have been surveyed and documented through the United States Department of Agriculture's National Cooperative Soil Survey program and show a wide diversity of soil types [USDA 28]. Hidalgo County, one of the 11 counties surveyed in this study, includes 13 general soil groups that can be further subdivided into 74 detailed soil-type units.[29] Extensive populations of SLN grow across a diversity of soil types in south Texas providing a prime setting to investigate the relationship between soil, plant health, and defenses. This study explores such correlations through a 50-site survey of SLN sub-populations over a 36,000 km^2 study area in the 11 southernmost counties of Texas. We investigated the interactions among soil type, population size, plant height, herbivory, and plant

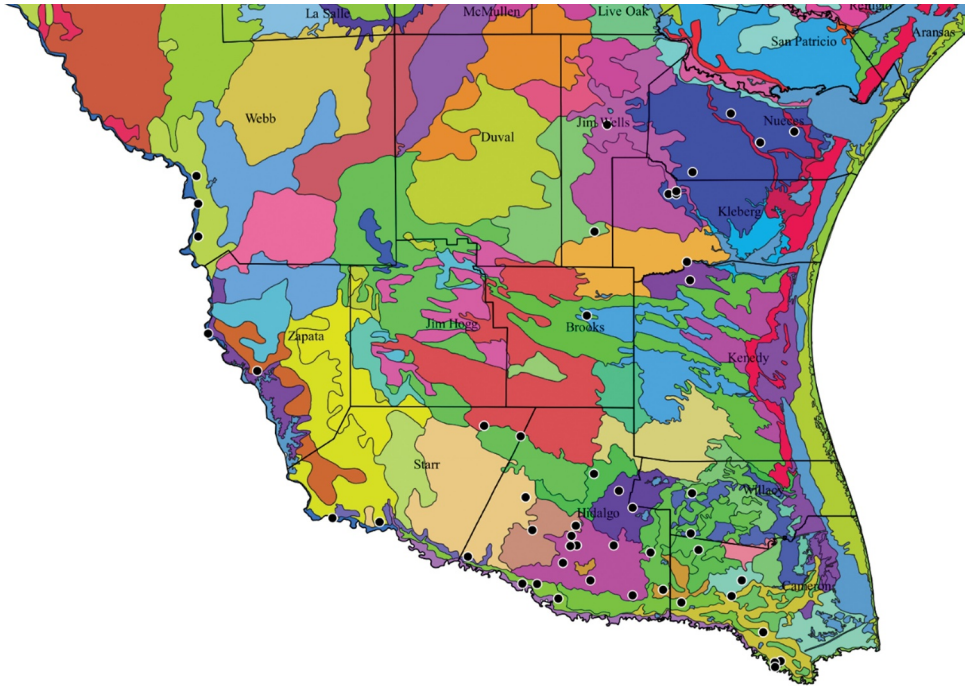

Figure 2. Map showing the sampling locations for the 50 subpopulations included in this study (black dots), their respective counties and the different soil types in that county. The survey area included 11 Texas counties and covered about 36,000 km^2.

defenses with the expectation that populations growing in the plant's preferred sandier soils would host larger colonies of healthier and better defended plants.

Material and methods

Sampling protocol

Fifty subpopulations of SLN were sampled across 11 south Texas counties in March, 2020 (Figure 2). At each sampling location, GPS coordinates, the scale of the subpopulation, and a brief location description were recorded. Ten plants that were at least 5–10 m apart (to reduce possible clonality, since SLN can spread through rhizomes) were randomly selected for height measurement, damage, visual assessment of type of herbivores feeding, and internode spine assessments. The damage assessment was recorded on a 0–4 scale where zero-plants had no damage, 1- had damage on one or two leaves, 2– on 25% of leaves, 3–50%, and 4–75% or more.[16] The visual insect assessment recorded the presence or absence of chewed holes and galls. Spines were assessed on a 0–2 scale where zero-plants had no spines, 1 – had moderate density of spines, and 2 – had very high spine density. In addition, stems were also sampled from three plants at each location and the number of spines per stem length, were assessed. Soil type was determined using the NRCS Web Soil Survey results for each of the location coordinates [USDA 28]. Detailed soil types are described in supplementary table as well as the simplified soil groups that were used for further analyses by soil type. The simplified soil classification included sand, clay, and urban for the analyses described for this study.

Statistical analyses

Plant height data were analyzed with fit model One-way Anova, with the three soil types as predictors. Post-hoc Tukey tests were carried out to tease out pairwise comparisons. All other response variables were on a scale (e.g., leaf damage 0–4) and considered as ordered data. We used ordered logistic regression and Wald tests to analyses these data sets.[30] More details on models and analyses are detailed in results. All analyses were carried out using JMP SAS (Statistical Analysis Software Institute, NC, USA) software and plots were made using GraphPad Prism version 15 (LA Jolla, California, USA). The map in Figure 2 was created using QGIS version 3.0 (Open-Source Geographic Information System) to show state county lines and soil type. Soil type was determined using the NRCS Web Soil Survey results for each of the location coordinates [USDA 28].

Results

Among the surveyed sites, soil type was significantly associated with plant height (One-way Anova; F = 7.06; P = .001). Pairwise comparisons suggest that *S. elaeagnifolium* in clay soils were significantly taller than the populations in sandy and urban soils (Figure 3). The ordered logit model developed for different damage levels of leaves is shown in Table 1A, including the coefficients of different soil types, cutoff thresholds (intercepts) and associated standard errors. The

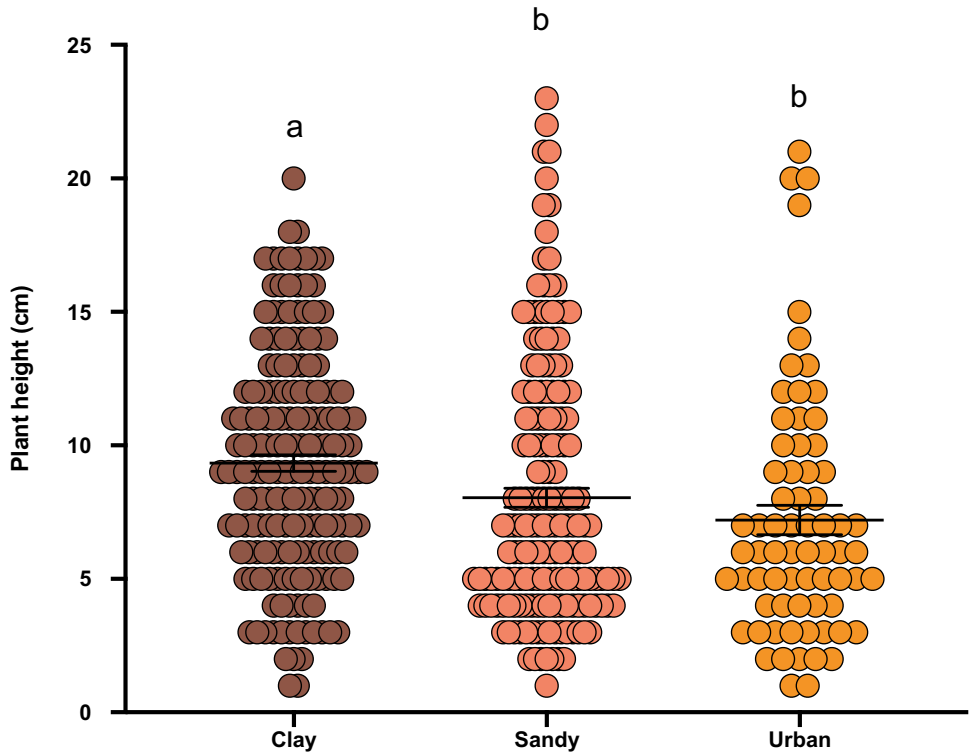

Figure 3. Results from our survey indicate that soil type had a significant effect on *Solanum elaeagnifolium* height (One-way Anova; F = 7.06; P = .001). Significant differences are based on post hoc Tukey tests represented by lowercase alphabetical letters at $P < .05$. The X-axis represents soil type and Y- axis plant height (cm).

Table 1.

Predictor	Coefficient	S.E.	Chi-sq	p
1A		**Leaf Damage vs Soil type**		
Intercept (0)	−0.9404	0.1165	65.2	<0.0001
Intercept (1)	0.9364	0.1158	65.33	<0.0001
Intercept (2)	2.1623	0.1565	191	<0.0001
Intercept (3)	3.9676	0.3252	148.87	<0.0001
Clay	−0.3816	0.1263	9.13	0.0025
Sandy	−0.2772	0.1264	4.81	0.0283
Wald chi-sq		16.2		0.0003
Psuedo R2		0.014		
AICc		1168.41		
BIC		1192.65		
1B		**Population Scale vs. Soil type**		
Intercept (0)	0.2414	0.1078	5.01	0.0251
Intercept (1)	2.0135	0.1563	165.81	<.0001
Clay	−0.1621	0.1321	1.51	0.2199
Sandy	0.7219	0.1421	25.8	<.0001
Wald chi-sq		28.7882		<0.001
Psuedo R2		0.0359		
AICc		780.98		
BIC		797.18		
1C		**Spines vs. Soil type**		
Intercept (0)	−1.0877	0.1211	80.74	<.0001
Intercept (1)	1.5449	0.1347	131.52	<.0001
Clay	0.5839	0.1352	18.66	<.0001
Sandy	−0.5154	0.1357	14.42	0.0001
Wald chi-sq		27.2221		<0.001
Psuedo R2		0.0324		
AICc		840.765		
BIC		858.963		

coefficients of the soil type shown in Table 1A are derived from the ordinal log-odds (logit) coefficients. The significance of soil type on damage levels were confirmed by the Wald χ2 test (Wald χ2 = 16.2; P = .0003). Table 1A shows that the odds of finding highest damage level is more in the plants in clay soils (β − 0.382) and the odds are lower in urban soils (β 0.66). The four intercepts in the table represent four cutoff thresholds that separate five different damage levels. Based on the standard error, none of the thresholds overlap, which indicates that the damage levels we considered in the study are significantly different from each other. Similarly, Table 1B shows that the odds of finding a higher population of the plants are more in urban areas (β − 0.56) and lower in sandy soils (β 0.7219). According to Table 1C, the odds of finding plants with highest number of spines are more in sandy soils (β − 0.5154) and odds are less in clay soils (β 0.5839). Both Table 1B and 1C shows significant effects of different soil types which was also confirmed with Wald χ2 tests. χ2 values of 28.78 ($p < .001$) and 27.22 ($p < .001$) were reported for population scale and spine analyses, respectively. Though the populations in clay soil were taller on average, they showed a lower concentration of spines than those in sandy soil, suggesting a trade-off between plant growth and defenses. Urban populations had intermediate spine intensity and did not differ significantly from the clay soils.

Discussion

In this study, we did a detailed sub-population survey of SLN in its native range in south Texas focused on the Rio Grande Valley at the border between the United States and Mexico. Our goal was to use the survey as a starting point to fill in missing details of its home range ecology, which only a few studies have undertaken.[12,13,16] Unlike observations in Australia and Greece, two highly invaded ranges

for this species,,[17,18,27] we did not observe a strong preference for sandy soils among the sub-populations in this survey, evident through our data on population size. Though more of our sites had sandy soils (54%) than clay (32%) or urban (14%) soils, the sandy sites had neither the largest populations nor the tallest plants (Table 1A-C). Sub-populations in clay soils, possibly due to better water and nutrient retention ability,[31] housed significantly more and taller plants.

Though sub-populations in sandier soils had fewer and shorter plants, they were better defended using internode spines as a defense index.[20,32] This pattern can be interpreted within the framework of growth-defense tradeoffs in plants. Plants respond to their environmental conditions and make resource allocation decisions to optimize their chances for reproductive success while defending against a suite of herbivores.[33,34] Our data suggest that genets in sandy sites have invested more into defenses at the possible expense of reproductive success, based on population size. It should be noted that the species propagates through rhizomes, and in a congener, we have previously found that a single mother can produce up to 21 sprouts in the following year.[35] However, this defense investment strategy did not translate in reduced herbivory at sandy sites when compared to clay sites. Our data gave us an overall estimate of growth and defense traits but did not quantify insect populations. To tease out the complexities of SLN's growth-defense tradeoffs in depth would require more information about the herbivore populations, magnitude of infestation and damage, their relationship with soil type, and subsequent influence on plant growth, reproduction, and defenses.[16]

Urban soils often experience high levels of anthropogenic disturbance.[36] SLN, like many weed species, thrives in disturbed environments. Traits like drought and heat resistance and easy spread through seed, rhizome, and root fragment enable it to rapidly colonize areas where other plants may struggle to take hold.[17,18] Ongoing disturbance like frequent mowing contributes to enhanced defense and fitness traits in both the plants that are mowed and subsequent generations.[16] Our data confirm the resilience of SLN to urban disturbance. Urban populations were significantly larger than those in sandy soil and they had the lowest leaf damage of all three soil categories. Urban plants were shorter but better defended by spines than clay populations. SLN's ability to survive and even be strengthened by mechanical and chemical disturbance complicates methods to control this noxious weed.

Invasive weeds exist within complex ecological systems in both their host and introduced ranges. Efficient management requires multidisciplinary approaches heavily informed by observations from the weed's native territory. Our results suggest that soil type does play a significant role in the establishment and defense strategies of SLN in its native range. Results from this survey will serve as the foundation for future research to better understand the relationships among soil, weed, and insect, and eventually translate these new ecological understandings into practical and effective control methods in the home and introduced ranges.

Acknowledgments

Special thanks to Vanessa Thomas for her assistance with the field survey and to Alejandro Vasquez for his work on the spine density assessment.

Disclosure statement

No potential conflict of interest was reported by the author(s).

Funding

This project was funded by the University of Texas Rio Grande Valley College of Sciences Seed Grant to Rupesh Kariyat, and USDA NIFA-HSI Grant # 2016-38422-25543 to Alexis Racelis.

ORCID

Lekshmi Sasidharan http://orcid.org/0000-0002-0788-6030
Rupesh Kariyat http://orcid.org/0000-0002-6565-6276

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