

Article

Solanum elaeagnifolium Invasiveness under Semi-Arid Environmental Conditions in Tunisia

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Abstract: *Solanum elaeagnifolium*, one of the world's most widespread invasive weeds, thrives in the regions of Tunisia with a semi-arid climate. An enhanced understanding of its biological traits could be useful for its management. For this purpose, *S. elaeagnifolium* vegetative propagation, flowering, fruiting, and spread patterns were assessed under semi-arid environmental conditions at Chott Mariem (Tunisia) over three years (2013–2015). Our results revealed that *S. elaeagnifolium* showed an active vegetative growth phase during the spring (March–May). Thereafter, the plant stopped its vegetative growth in June–August in favor of flowering and fruiting. The vegetative growth resumed during September–October and declined in November, announcing its dormant period. Thanks to its vigorous rhizomatous system, *S. elaeagnifolium* was able to emit offshoots within a radius of 1.5 m from parent shoots by 30 months after its establishment. These findings could inform and improve dedicated management control options for *S. elaeagnifolium*. Silverleaf nightshade should be controlled before the full-flowering stage in spring and following the first autumnal rainfall to prevent vegetative propagation and fruiting.

Keywords: plant traits; silverleaf nightshade; Tunisia; vegetative propagation; weed control



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1. Introduction

Invasive alien plants represent a major threat to agricultural and natural systems and to an ecosystem's services and functioning. Their impacts can be intense, insidious and might produce irreversible ecosystem changes [1–4]. Furthermore, it is commonly assumed that invasion by alien plants may result in biotic homogenization [5], directly threatening biodiversity, e.g., by displacement of native flora, and indirectly through placing natural resources under strain [2,6,7].

Solanum elaeagnifolium Cav. (silverleaf nightshade) is a deep-rooted, summer-growing perennial herb of the Solanaceae family, with an amphitropical native distribution, occurring in the deserts and dry zones of the northern hemisphere in the southwestern United States of America and Mexico, and in the southern hemisphere in Argentina, Paraguay, Uruguay, and Chile [8,9], and [8,10] is now widely naturalized beyond its native range; therefore it is considered one of the world's most widespread invasive weeds [8,11–14]. It is invasive mainly in crops and orchards, but also in other types of land uses, such as uncultivated fields, pastures, roadsides, waste lands and, locally, in forest edges [14] in several temperate, semi-arid, and sub-tropical regions [4,15–21]. It may compete with native plant species for pollinators [22], successfully compete with native ruderal species of the Mediterranean, such as *Cichorium intybus* [11,23], and become dominant in plant communities in overgrazed rangeland and heavily trampled areas around waterholes. However, its environmental impacts are generally considered limited in comparison with its impacts on cultivated lands [12,22]. Its first records in North Africa date back to 1940 in Morocco, 1956 Egypt, and 1999 in Algeria [24].

In Tunisia, *S. elaeagnifolium* was first detected in 1985 at Sbikha in the governorate of Kairouan (central Tunisia) [25]. Since then, its distribution has been increasing, and

the species was detected in many other governorates (Sousse, Mahdia, Sidi Bouzid, Sfax, and Zaghouan) [26]. Silverleaf nightshade is now recognized as an invasive alien weed of agricultural land, mainly in arid and semi-arid regions [27]. As in the other parts of the Mediterranean basin, the most infested habitats and land-uses are roadsides, waste lands, and irrigated summer crops [27,28]. In a few years, the species became a successful invader. In fact, short- and long-distance dispersal are facilitated by human activities, water, birds and other animals, vehicles, and machinery. Seeds can be spread in the feces of a variety of animals, including cattle and sheep [29]. Therefore, grazing is a poor method of control, as 10% of seeds that pass through the gut remain viable and take up 2 weeks to be excreted, making this a mandatory ‘clean out’ period before stock can be moved to uninfested areas [30].

According to Ref. [27], silverleaf nightshade invasiveness in Tunisia could be related to its plant traits, such as its copious production of sexual and asexual propagules; facility for long-distance dispersion; ability to endure considerable drought and to dominate shallow-rooted vegetation, especially during summer dry periods; and its capacity to outcompete more valuable species because it is unpalatable and toxic to cattle [27]. Furthermore, its invasion is facilitated by irrigation and animal husbandry practices, including the spread of contaminated manure [12]. Low-moisture stress may favor this invasive species, and sheep are an important pathway for its long-distance dispersal [27].

However, despite silverleaf nightshade being widespread in Tunisia, there is very little documented knowledge and quantitative information on the drivers of its invasiveness, which makes its effective management challenging. Our research aimed to assess the most important traits that make *S. elaeagnifolium* a successful invader in Tunisia and to identify possible management actions.

2. Materials and Methods

We conducted the field experiment from June 2012 to December 2015 in experimental plots at the Higher Agronomic Institute of Chott Mariem. The region of Chott Mariem is situated in central-eastern Tunisia, between 35°90′–35°99′ N and 10°50′–10°60′ E (Figure 1).

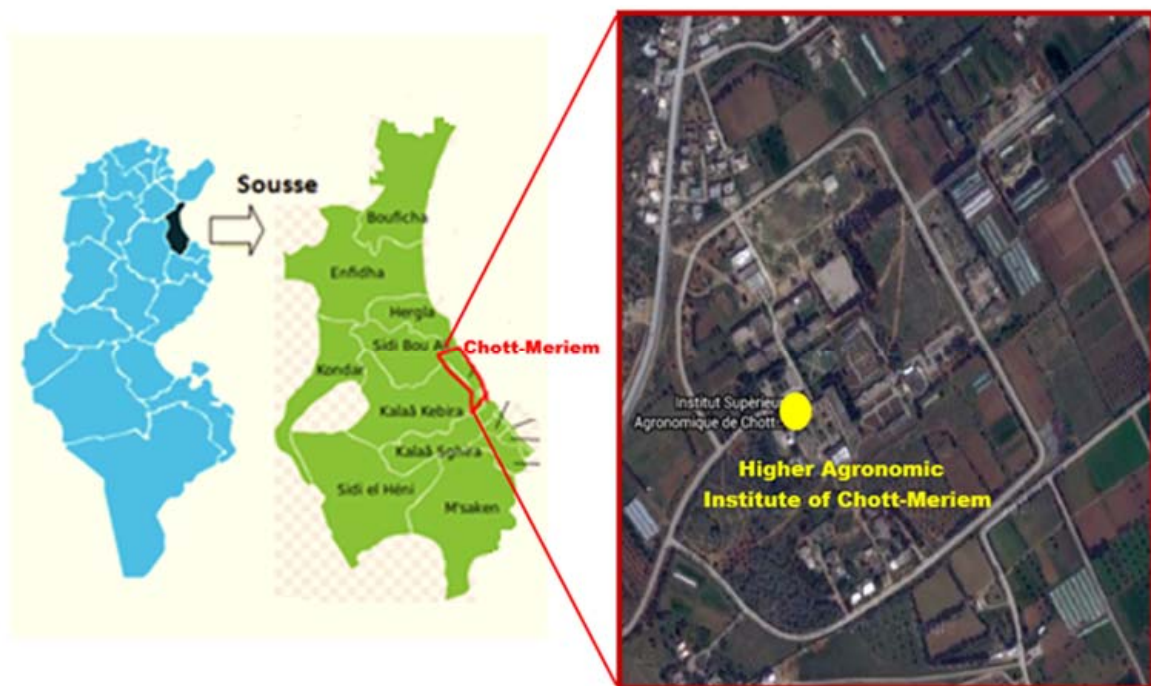


Figure 1. Map of study site (Chott Mariem, Sousse, Tunisia).

The region of Chott Mariem is characterized by a semi-arid climate with mild rainy winters, hot dry summers, and a great annual and seasonal variability in precipitation. During the years 2011–2015, the region received an average annual rainfall of 350 mm (Table 1). However, there is a strong annual and seasonal variability of rainfall. In general, precipitations are the heaviest in autumn.

Table 1. Average monthly rainfall (mm) in Chott Mariem, Sousse.

Year	Jan	Feb	Mar	Apr	May	Jun	Jul	Ago	Sep	Oct	Nov	Dec	Tot
2011	32.5	35.7	40.5	32.4	60.0	31.5	0.0	0.0	0.0	135.5	67.0	20.5	455.6
2012	32.0	55.2	80.1	15.0	7.2	0.0	0.0	6.5	81.5	8.0	0.0	0.0	285.5
2013	14.0	19.0	44.5	8.0	0.0	0.0	0.0	8.0	23.5	29.5	27.0	94.7	268.2
2014	6.3	5.4	9.7	2.7	2.7	3.9	0.0	0.1	18.7	3.5	13.4	41.7	108.1
2015	0.0	40.0	39.5	0.0	0.0	0.0	3.0	79.0	33.0	39.0	40.0	22.3	295.8

The coastal plain of Chott Mariem is characterized by a very low slope. The waters of the shallow aquifer of the plain are generally subject to intense exploitation, which resulted in a decrease in piezometry and increased salinity. The soil in the study plot has been described in three horizons, namely [0–20 cm], [20–40 cm], and [40–60 cm], since there was a change in color of the layers at different depths [31]. According to the USDA 1951 classification, the soil is a sandy clay loam (Fluvisol soils) with a pH value in the range 7–8 and an EC value (mS/cm) in the range 0.75–0.85, with very similar values in the three horizons due to cultivation.

We collected two hundred *S. elaeagnifolium* vertical tap root fragments (5 cm length) in June 2012 from an infested field at Chott Mariem. We buried each fragment at 5 cm depth into 12 cm-diameter pots, filled with a mixture of black peat (50%), sand (30%), and perlite (20%). We placed pots in a greenhouse and watered regularly. During September 2012, we transplanted 160 plants, at the stage of 2–4 leaves, into a tilled open field. We transplanted these plants in five rows with 2 m intra- and inter-spacings. Because of the scarcity of precipitation during the autumn (Table 1), we irrigated transplants once a week in September–November to enhance their establishment.

We monitored the following five *S. elaeagnifolium* plant traits monthly, from March to December, during three growing cycles (2013, 2014, and 2015): (i) vegetative regeneration rate, calculated as the number of regenerated new shoots from old stems (Figure 2); (ii) vegetative propagation rate, calculated as the number of lateral offshoots emerged from rhizomes (Figure 1); (iii) vegetative spread, estimated as the product of the number of lateral offshoots emerged from rhizomes per the average distance from the parent plants; (iv) flowering potential, calculated as the total number of flowering shoots per month; and (v) fruiting potential, calculated as the total number of fruiting shoots per month.

We performed data analyses and visualizations using R-Studio version 4.0.3 (<https://www.r-project.org/> (accessed on 1 July 2022)), R packages MASS [32] for GLMs models, and ggplot [33] for data visualization.

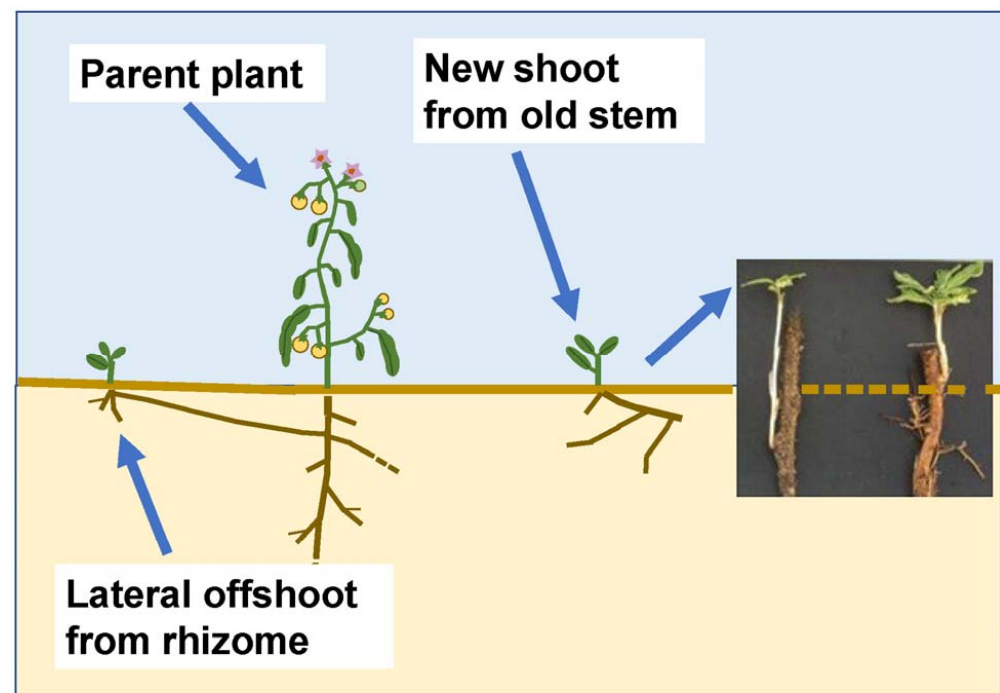


Figure 2. Illustration of *Solanum elaeagnifolium* showing new shoots produced by old stems and lateral offshoots emerging from rhizome.

3. Results

Solanum elaeagnifolium showed a post-transplantation survival rate of 100% in the open field during its establishment season in autumn 2012. Thereafter, *S. elaeagnifolium* aerial parts dried up due to winter frosts.

At the beginning of the first growing cycle (March 2013), 55 new shoots regenerated from old stems (Figure 3). This means that approximately 35% (55 regenerated new shoots from 160 transplanted plants in autumn 2012) of *S. elaeagnifolium* transplanted plants were able to regenerate new shoots in March 2013. New shoots regeneration lasted from March to May 2013, stopped from June to August, and restarted from September to October. Later in November, new shoots regeneration declined, announcing the winter dormant period (December–February), during which some dried shoots stand with mature berries.

At the beginning of the second growing cycle (March 2014), the number of new shoots regenerated from old stems was 2.2 times higher than that recorded in March 2013 (from 55 to 120) (Figure 3). In fact, unlike the first growing cycle during which there was a weak new shoots regeneration, the second growing cycle was characterized by an active vegetative propagation with two peaks, the first in spring (March–May) and the second in autumn (September–October). Thereafter, during the third growing cycle (March–December 2015), we observed the same regeneration trend, and the two vegetative regeneration peaks were confirmed. These findings support that *S. elaeagnifolium* vegetative propagation, calculated as the number of regenerated new shoots from old stems, varied depending on the seasons and had a relationship with the environmental conditions in the study site.

Silverleaf nightshade vegetative propagation results revealed that during the first growing cycle (2013), the emergence of lateral offshoots from rhizomes (daughter plants) occurred only in autumn, with 12 and 10 lateral offshoots in September and October, respectively (Figure 3). However, in 2014 and 2015, lateral offshoots emergence from rhizomes was observed twice during each growing cycle. In 2014, the first emergence period of lateral offshoots began in April, peaked in May, and decreased in June. The second emergence period occurred during September–October. In 2015, the first emergence period began earlier in March, peaked in April, and decreased in May. The second emergence period occurred during September–October.

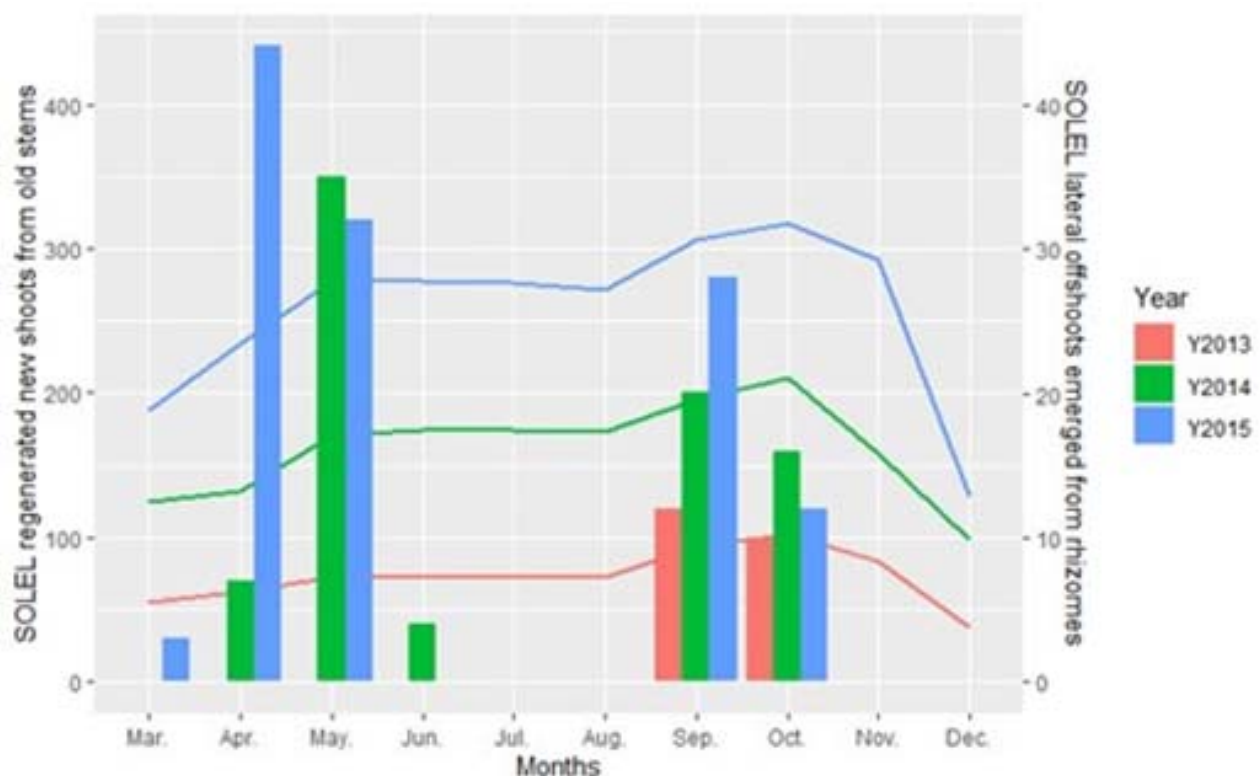


Figure 3. *Solanum elaeagnifolium* new shoots regeneration from old stems and lateral offshoots emergence from rhizomes during three growing cycles (2013, 2014, and 2015), following its transplantation in an open field at Chott Mariem, Tunisia, in autumn 2012.

The number of emerged lateral offshoots from rhizomes during the first growing cycle (2013) was very limited—12 lateral offshoots emerged close to parent shoots (<5 cm) (Figure 4). Thereafter, the distance of lateral offshoots emergence from parent shoots reached 100 cm and 150 cm after 18 and 30 months, respectively, after the transplantation in the open field in September 2012.

The results of GLM analysis highlighted that vegetative spread was significantly different among years ($p = 0.007$ and $p = 7.13 \times 10^{-13}$ for 2014 and 2015, respectively) and parent plants. In the analysis, vegetative spread was estimated as the product of the number of lateral offshoots emerged from rhizomes per the average distance from the parent plants.

Silverleaf nightshade flowering potential (calculated as the total number of flowering shoots per month) results highlighted that during the first growing cycle (2013), flowering started in May when 50 flowering shoots were observed; furthermore, this number peaked in June with an increase of about 40%, and it declined in October (Figure 5). Nevertheless, in 2014 and 2015, flowering started earlier in April. In 2014, the flowering shoots number peaked in July (171 flowering shoots); thereafter, it declined in October. However, in 2015, the flowering shoots number peaked in June with an increase of about 61% and 290% in 2014 and 2013, respectively. These results showed that *S. elaeagnifolium* flowering potential varied according to the year, and the length of the flowering period varied during the three growing cycles (2013, 2014, and 2015). This variation could be related to the plant's response to the environmental site characteristics.

The assessment of *S. elaeagnifolium* fruiting potential (calculated as the total number of flowering shoots per month) revealed that the fruiting period occurred in the same period during the three growing cycles. It started in June, peaked in August, and declined in November (Figure 6). In August 2015, the fruiting shoots number was higher than in 2014 and 2013, with increases of about 53% and 280%, respectively.

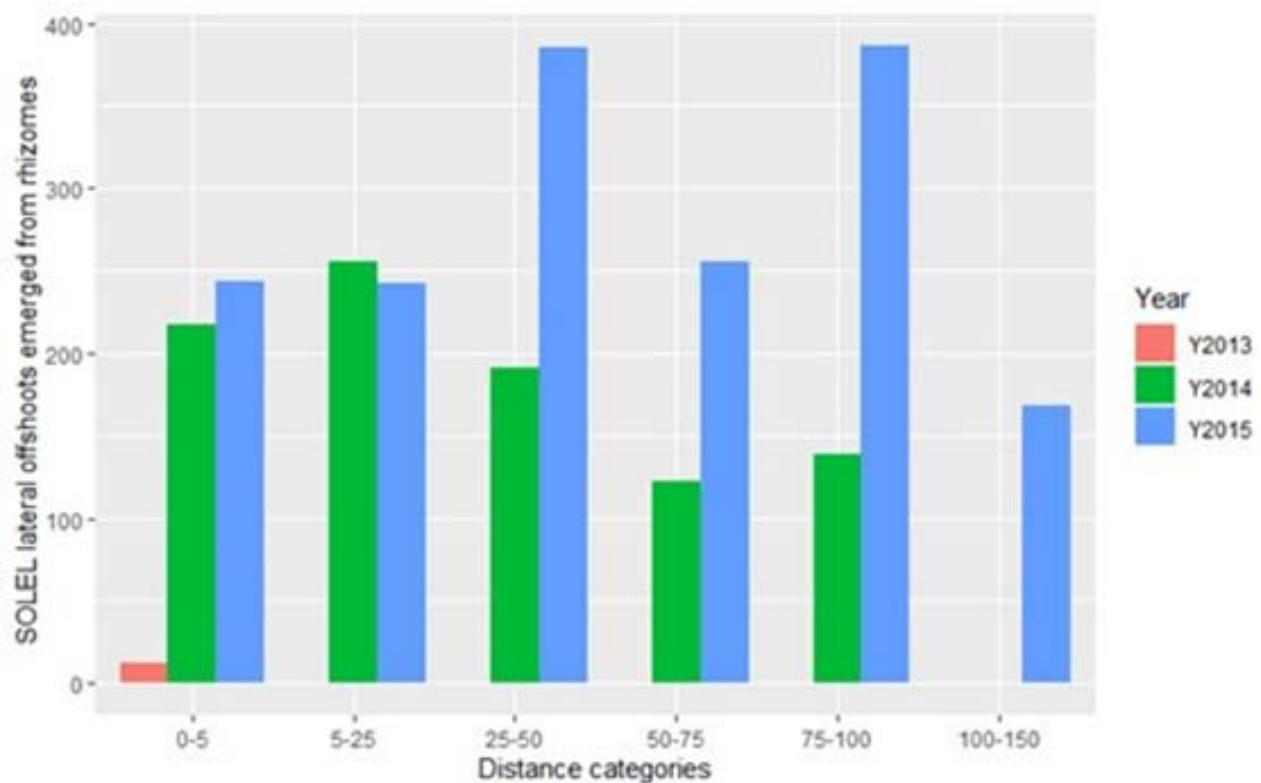


Figure 4. *Solanum elaeagnifolium* lateral offshoots number at six distance categories (0–5, 5–25, 25–50, 50–75, 75–100, and 100–150 cm) from parent shoots during three growing-cycles (2013, 2014, and 2015) in Chott Mariem.

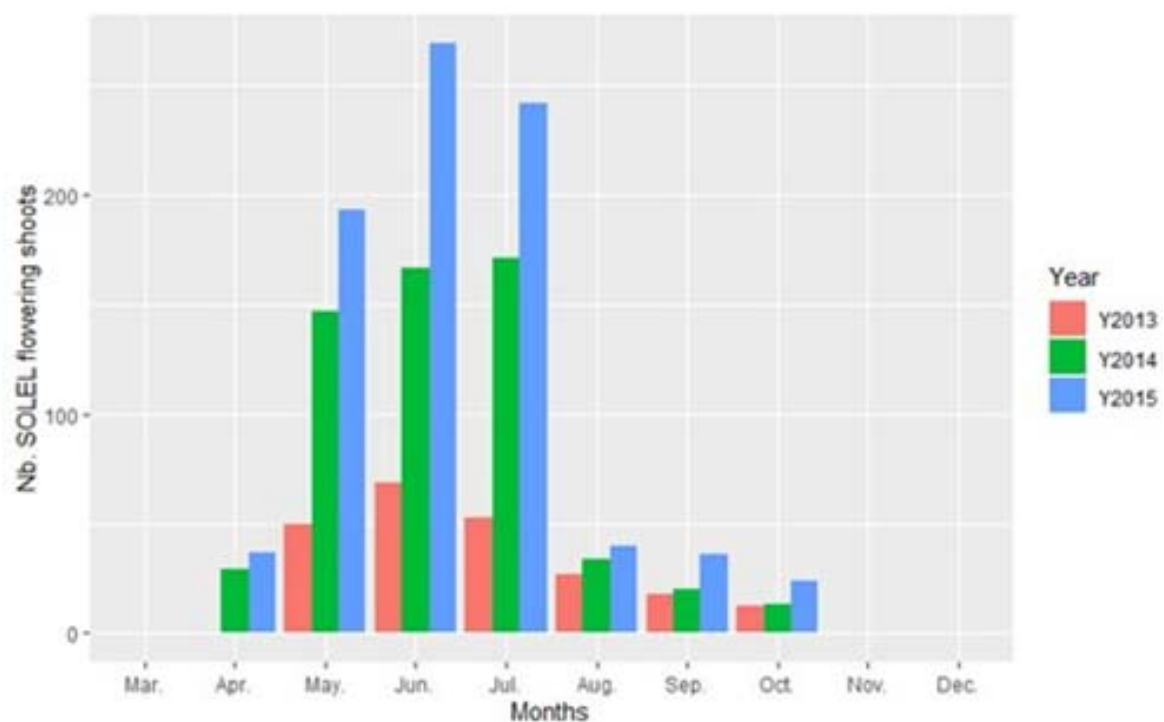


Figure 5. *Solanum elaeagnifolium* flowering potential, calculated as the total number of flowering shoots per month, during three growing cycles (2013, 2014, and 2015) at Chott Mariem, Tunisia.

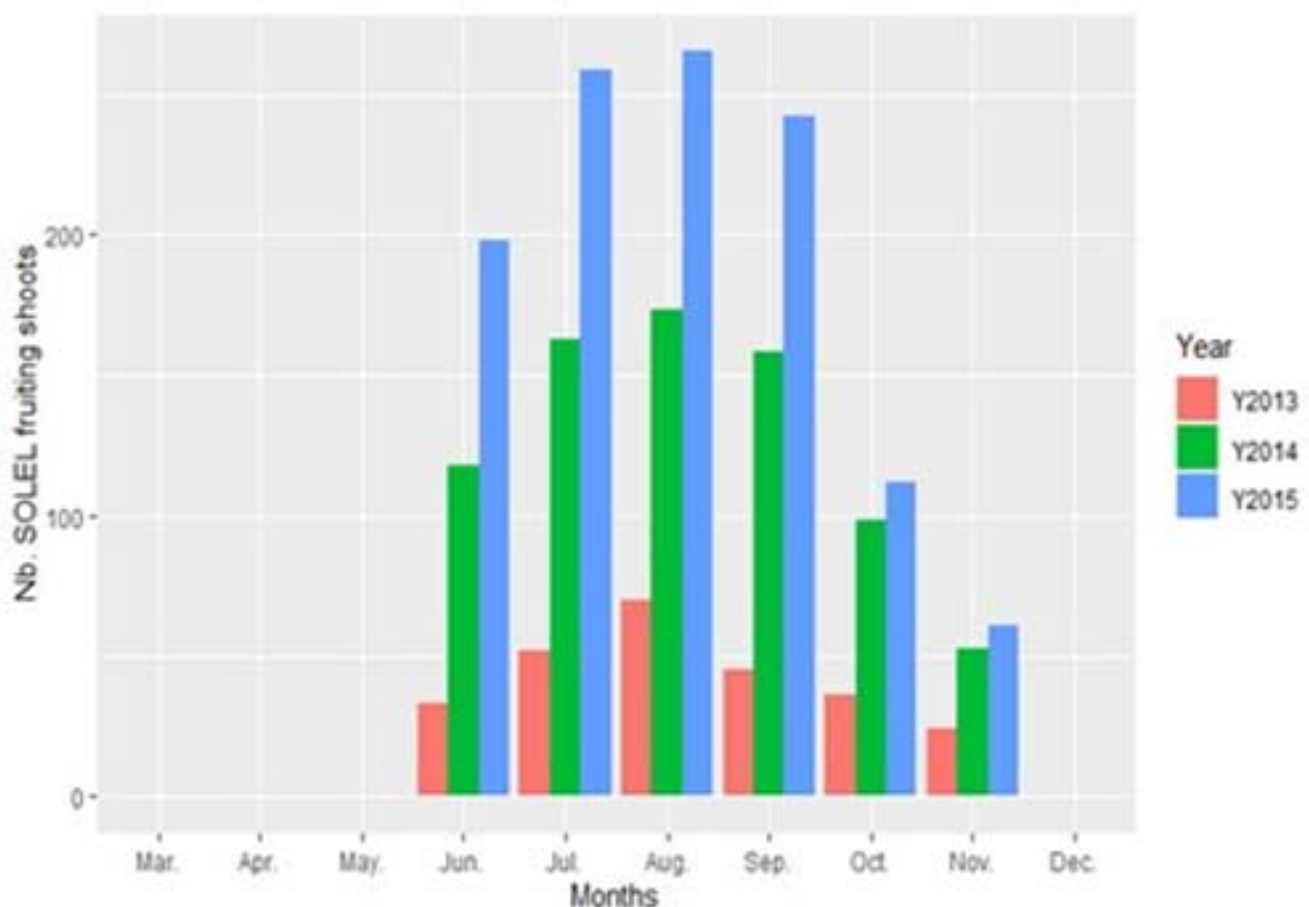


Figure 6. *Solanum elaeagnifolium* fruiting potential, calculated as the total number of fruiting shoots per month, during three years (2013, 2014, and 2015) at Chott Mariem, Tunisia.

4. Discussion

Solanum elaeagnifolium is one of the most invasive plant species worldwide and it colonizes crops and human-disturbed land. The success of this invasive alien plant is generally attributed to differences in its functional traits compared with less successful aliens and native species and crops in the invaded communities. Invasion processes are driven by an interplay between the invading species and communities [13]. However, in this study we focused only on a selected group of *S. elaeagnifolium* plant functional traits; therefore, this should be considered only as part of the preliminary general framework to prepare dedicated action plans. We are also aware of the main observational nature of the study, which was performed in a single site, although it is representative of the silverleaf nightshade invasive range in Tunisia and other northern African countries.

Overall, our results showed the high vegetative regeneration, propagation, and spread of silverleaf nightshade (Figure 7) in accordance with previous studies supporting the high viability of *S. elaeagnifolium* root fragments [10,13,27] and the fact that root stocks less than 1 cm-long can regenerate into plants [34,35]. Root fragments produced a kind of root bank in the soil, and around 40% of *S. elaeagnifolium* root fragments that did not regenerate during the first growing cycle regenerated after nearly 18 months.



Figure 7. *Solanum elaeagnifolium* successful establishment in the experimental site (Chott Mariem, Tunisia, 2015).

Thanks to its vigorous rhizomatous system, silverleaf nightshade was able to produce lateral offshoots far from parent plants within a radius of 1.5 m 30 months after its transplantation in the open field. This highly competitive clonal growth pattern is an important characteristic that enhances the success of alien plants in new habitats. These conclusions are in accordance with many previous studies that documented how plants capable of both sexual and vegetative propagation may have an advantage against plants that reproduce only sexually [36–38]. Indeed, this study highlighted the role of the vegetative propagation as a determinant factor of *S. elaeagnifolium* invasiveness and underlined its importance during establishment, even under very restrictive climatic conditions. In fact, in the study site, drought was not a limiting factor for *S. elaeagnifolium* vegetative propagation, which is consistent with Ref. [39], which showed that *S. elaeagnifolium* tolerates climates with relatively high summer temperatures and low annual rainfall. This weed is adapted to semi-arid regions with 300–600 mm annual rainfall and coarse textured, sandy soils [10,13,27]. In Morocco, ecological conditions linked to the climate and altitude affect *S. elaeagnifolium* distribution, and it was observed that the most severe climate and altitude conditions favor the abundance of the most invasive populations [40].

Despite some time lag between the three growing cycles (2013, 2014, and 2015), our results revealed that, under the semi-arid conditions at Chott Mariem, the *S. elaeagnifolium* biological cycle was characterized by two active vegetative growth phases, the first during spring (March–May) and the second during autumn (September–November). During the summer period (June–August), the plant stopped vegetative growth in favor of sexual reproduction (flowering and fruiting). In fact, flowering started in April, peaked in June,

and declined in October. Fruiting started in June, peaked in August, and declined in November. During winter (December–January–February), *S. elaeagnifolium* aerial shoots are dried up by winter frost; nevertheless, rhizomes remained alive and ensured plant regeneration in the next spring.

Overall, these findings could help to improve dedicated management plans to control *S. elaeagnifolium* in Tunisia. During spring, i.e., the most intense growing period in Tunisia, chemicals or other mechanical/physical methods should be applied to inhibit and/or slow down the vegetative growth of this alien weed. In fact, chemical control of silverleaf nightshade is quite well documented in the literature [13,41–43].

Consequently, during summer, mechanical control would be required to decrease weed density, control fruiting, and prevent long-distance dissemination. In autumn, chemical treatments could be more appropriate to control regeneration in the next spring, as suggested by several studies [41,42,44]. For perennial weeds such as *S. elaeagnifolium*, the best time for the application of systemic herbicides should coincide with the period of carbohydrate storage in underground organs. However, the control of *S. elaeagnifolium* remains highly challenging and, whenever possible, preventive methods should be applied to avoid the infestation of new land. In fact, recent studies [45] showed that mowing exerts a selective pressure that enhances some fitness and defense traits in *S. elaeagnifolium* and can contribute to producing superweeds. At the same time, herbicide-resistant weeds may easily arise and would pose a significant challenge to sustainable food production. Plant traits are assumed to play a significant role in determining whether a weed is likely to evolve herbicide resistance but there have been few quantitative assessments to date [46].

5. Conclusions

Solanum elaeagnifolium has already invaded and is currently spreading in both natural and disturbed habitats in arid and semi-arid regions in Tunisia. Overall, the present study confirmed the high viability of *S. elaeagnifolium* root fragments, in addition to its capability to generate new shoots from old stems. On the other hand, the study highlighted the role of vegetative propagation as a determinant factor of the local establishment of *S. elaeagnifolium* under very restrictive climatic conditions. In fact, thanks to its vigorous rhizomatous system, the plant can produce lateral offshoots far from parent plants and rapidly reach high coverage values. These results should support the drafting of regional or national integrated action plans and phytosanitary measures to control *S. elaeagnifolium*, limit its spread, and prevent future invasion in new agricultural areas in Tunisia. Silverleaf Nightshade is very difficult to control once established, its spread can occur both vegetatively from cut root sections and via seed by agricultural practices; therefore, it is essential to keep it out of uncontaminated areas and adopt good practices to avoid its spread from infested areas.

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