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Review:
Ecological impact and bioactive profile of the invasive species *Solanum elaeagnifolium* in the Gaza Strip, Palestine

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Abstract. *Abou Auda M, Eleyan M. 2025. Review: Ecological impact and bioactive profile of the invasive species* Solanum elaeagnifolium *in the Gaza Strip, Palestine. Biodiversitas 26: 3485-3513. Solanum elaeagnifolium* (Silverleaf nightshade) is an aggressive invasive species in the Middle East, particularly in the Gaza Strip, Palestine, where it poses significant ecological and agricultural threats. This review provides a comprehensive analysis of the botany, ecology, phytochemistry, pharmacology, and toxicology of *S. elaeagnifolium* in the Gaza Strip. It is the first study to focus on its invasive potential and bioactivity in this region, with an emphasis on the need for monitoring and effective control strategies. A comprehensive literature review was conducted, sourcing data from PubMed, Scopus, Web of Science, and Google Scholar databases up to April 2025. The plant contains flavonoids, glycoalkaloids, phenolic acids, and saponins. Nutritional content includes crude fiber (28-32% in leaves; 27-32% in flowers), protein (13-14%), potassium (2.6% in leaves; 3.3% in flowers), and phosphorus (0.21-0.24%). Toxicological studies reported hepatotoxic effects at 2000 mg/kg fruit extract ($p<0.001$), elevated ALT/AST and creatinine ($p<0.01$), and altered RBC counts. Antioxidant activity showed DPPH IC_{50} of 0.025 mg/mL (seeds) and 35.15 µg/mL (fruit). Enzyme inhibition assays revealed lipase IC_{50} of 0.167 mg/mL (leaves) and 0.106 mg/mL (fruit), and antiglycation IC_{50}: 3.997 mg/mL. Antimicrobial assays showed broad-spectrum activity, with inhibition zones ranging from 12-20 mm and MIC values of 1.25-2.5 mg/mL against multiple gram-positive and gram-negative bacteria. Ecologically, *S. elaeagnifolium* develops an extensive root system and vigorous rhizome spread, which significantly enhance its invasiveness. *Solanum elaeagnifolium* presents a significant ecological threat in the Gaza Strip, with its invasive behavior driven by its deep root system and vigorous rhizome spread. Preliminary phytochemical screening indicates the presence of alkaloids and saponins, warranting further in vitro validation. The plant's bioactive properties, such as its antimicrobial and antioxidant activities, suggest its potential for pharmacological applications. However, further experimental studies are needed to assess the clinical viability and toxicity of these compounds.

Keywords: Invasive species, phytochemistry, silverleaf nightshade, *Solanum elaeagnifolium*, weed

INTRODUCTION

Medicinal plants are known to be rich in natural bioactive compounds, and many of these substances have been utilized to develop various pharmaceutical products with anticancer, antidiabetic, and cardioprotective properties (Ibrahim et al. 2022b; Chaachouay and Zidane 2024). Several species of this genus are used in traditional medicine and have demonstrated potential therapeutic effects against metabolic disorders, microbial infections, inflammation, and oxidative stress (Umamageswari et al. 2017; Peng et al. 2020; Aabideen et al. 2022; Bouslamti et al. 2023; Nderitu et al. 2023). In addition, the rich content of flavonoids and polyphenols in Solanum extracts exhibits antioxidant and anti-inflammatory properties, protecting biological systems from oxidative stress (Campisi et al. 2019; Yeom et al. 2019). In Palestine and Jordan, its extracts demonstrate antimicrobial activity comparable to traditional medicines (Qasem 2014; Navarrete et al. 2015; Al-Hamaideh et al. 2020).

Among these, *Solanum elaeagnifolium* is a species of particular interest. Although native to North America, it has proven to be highly invasive in other regions, such as the Gaza Strip, Palestine. Due to the military conflict and widespread destruction of arable land in the Gaza Strip, *S. elaeagnifolium* has rapidly colonized disturbed and abandoned agricultural areas (Sayari et al. 2022). Its adaptability to stressful environments, coupled with its aggressive invasiveness (Kobisi et al. 2024). In Tunisia and Morocco, its allelopathic effects suppress crops (Balah et al. 2022), where it colonizes roadsides, orchards, pastures, overgrazed rangelands, and other disturbed habitats (Uludag et al. 2016; Qasem et al. 2019; Ghabrit et al. 2020; Kumar and Singh 2020; Sayari et al. 2022). This pattern is consistent with observations in other Mediterranean and arid regions, where invasive Solanaceae species often present a similar dual challenge as ecological disruption alongside potential ethnobotanical or pharmacological utility, such as *Solanum nigrum* in the Mediterranean Basin, *Solanum rostratum* in parts of Africa (Gafforov et al. 2024). *Solanum elaeagnifolium* exemplifies this dual potential. On one hand, it reduces biodiversity and interferes with crop production; on the other, it may provide an abundant, accessible source of therapeutic phytochemicals (Karmezi et al. 2023; Lenda et al. 2023), especially in regions like Gaza Strip where pharmaceutical access is limited. This review aims to articulate this paradox, exploring *S. elaeagnifolium* not only as an ecological threat but also as a potential source of valuable bioactive compounds, justifying its relevance in the local context of the Gaza Strip (Figure 1).

The ecological success of *S. elaeagnifolium* in these regions is strongly linked to its biological traits. It produces both sexual and asexual propagules in large quantities, enabling effective local and long-distance dispersal (Roberts and Florentine 2022). Studies in Tunisia and Jordan revealed that vegetative propagation occurs actively in spring and autumn, while lateral rhizomatous offshoots can spread up to 1.5 meters from parent shoots within 30 months (Gagnon et al. 2023). This clonal spread makes it extremely difficult to contain once established and enhances its ability to exploit ecological disturbances. These characteristics are highly relevant to the Gaza Strip, where similar semi-arid conditions prevail, compounded by conflict-driven landscape degradation (Sayari et al. 2022).

This paradox highlights an emerging need to reassess the role of invasive flora not only as threats but also as possible contributors to public health resilience. In conflict-affected regions, local medicinal plants may be critical in supporting primary healthcare and alternative treatment strategies. Furthermore, the ecological adaptability of *S. elaeagnifolium* suggests a robust internal antioxidant defense system, which may be reflected in its chemical makeup (Tataridas et al. 2023). Plants that thrive under stress, drought, salinity, or soil degradation often synthesize secondary metabolites, such as flavonoids and terpenoids, as defense mechanisms (Emami et al. 2024). These compounds are frequently the same ones responsible for the plant's pharmacological effects.

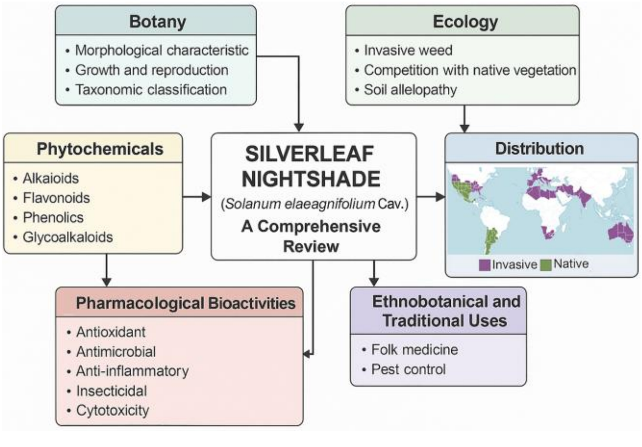

Figure 1. Conceptual diagram illustrating the core thematic domains addressed in this review of *Solanum elaeagnifolium*. The diagram shows the plant's botany, ecology, phytochemicals, pharmacological bioactivities, ethnobotanical and traditional uses, and distribution (Al-Hamaideh et al. 2020; Bouslamti et al. 2022b, et al. 2023)

Recently, increasing attention has been devoted to the floristic analysis, diversity, taxonomy, and ecology of the vascular flora of Palestine, including the Gaza Strip, West Bank, and Jerusalem. More specifically, researchers have shown greater interest in studying plant diversity, systematics, ecological characteristics, and the phytochemical and proximate analysis of wild plants in the Gaza Strip (Ali-Shtayeh et al. 2015; Dardona 2016; Abd Rabou and Radwan 2017; Ighbareyeh et al. 2017; Ali-Shtayeh and Jamous 2018; Ighbareyeh and Carmona 2018; Abou Auda et al. 2022; Ali-Shtayeh et al. 2022; Ighbareyeh et al. 2022; Abou Auda 2023; 2025a; Abou Auda et al. 2023; Abd Rabou et al. 2024; Abou Auda et al. 2024; Abou Auda and Ighbareyeh 2024). Meta-analyses have shown that a number of invasive species play an important role in drug discovery, especially in regions with limited access to medicines (Atamaleki et al. 2022). A re-evaluation of such species in terms of ecological control and biomedical potential is therefore required in both conservation biology and ethnopharmacology.

Although several studies have investigated the pharmacological or ecological aspects of *S. elaeagnifolium* in general, to our knowledge, no previous study has focused specifically on the integrated ecological, botanical, chemical, and therapeutic profile of this species in the Gaza Strip or comparable conflict-affected arid ecosystems. The present review aims to fill this gap by summarizing the available data, focusing on the phytochemical richness, local nutritional value, toxicity profiles, and bioactive potential of *S. elaeagnifolium* in this unique regional context. Specifically, the objectives of this review are: (i) to document the ecological behavior and invasive potential of *S. elaeagnifolium* in the Gaza Strip; (ii) to compile and analyze its ethnomedicinal uses and traditional knowledge; and (iii) to systematically review its phytochemical composition, nutritional content, toxicological profiles, and pharmacological activities as reported in the literature. It addresses an urgent ecological challenge while also highlighting the biomedical potential of the plant as a locally available resource in underserved health systems.

BOTANICAL CHARACTERISTICS AND TAXONOMY

Morphological description

Solanum elaeagnifolium is a perennial herb or subshrub reaching 20-150 cm in height, characterized by its deep rhizomatous root system, which enables both sexual and vegetative reproduction and contributes to its invasive capacity in arid regions (Figures 2 and 3; Tables 1 and 3) (Roberts and Florentine 2022; Tataridas et al. 2023). The plant exhibits erect, or creeping stems covered with stellate trichomes, giving it a silvery-green appearance, and often bears scattered prickles (Knapp et al. 2017). Leaves are alternate, simple, and vary in shape from lanceolate to ovate, densely hairy on both surfaces. The inflorescences are typically axillary or terminal umbels bearing violet to bluish five-lobed hermaphroditic flowers, followed by yellow to orange berries containing numerous flattened seeds (Knapp et al. 2017; Qasem et al. 2019; Roberts and Florentine 2022). Notable morphological variation across populations including differences in leaf shape, flower color, and trichome density is likely driven by underlying genetic diversity (Knapp et al. 2017; Roberts and Florentine 2022). These traits, combined with its persistent growth cycle and tolerance to stress, make it highly adaptable to disturbed habitats such as those in the Gaza Strip (Figures 2 and 3). This morphological versatility, particularly its deep root system and rhizomatous propagation, contributes significantly to its invasive potential in arid and semi-arid habitats. These traits allow the plant to regenerate after mechanical disturbance and persist under prolonged stress conditions such as drought, overgrazing, and low soil fertility, which are common in the Gaza Strip and other Mediterranean drylands. Morphologically, it is often confused with other members of the genus *Solanum*, as it shares common features such as stellate trichomes and prickles. However, recent molecular studies have clarified its phylogenetic position. DNA barcoding with nuclear (waxy) and chloroplast regions (*matK* and *trnL-trnF*) successfully distinguished *S. elaeagnifolium* from closely related species within the genus (Zhu et al. 2018). In addition, sequencing of the chloroplast genome has shown that *S. elaeagnifolium* is closely related to species in the Melongena section of the Leptostemonum clade, providing valuable phylogenomic context (Zhu et al. 2020). These molecular findings support the distinct taxonomic identity of the species and support its classification within the highly diverse family Solanaceae. Clarifying the taxonomic status of *S. elaeagnifolium* is not only important for botanical classification but also essential for designing species-specific control strategies. Its phylogenetic closeness to other medicinally valuable *Solanum* species also raises interest in its potential phytochemical overlap and bioactivity, which may contribute to both its ecological dominance and pharmacological relevance.

Taxonomic classification

Solanum elaeagnifolium is a eukaryotic plant in the kingdom Plantae, division Spermatophyta, class Angiospermae, subclass Magnoliopsida, order Solanales, family Solanaceae, genus *Solanum*. *Solanum elaeagnifolium*, a member of the Elaeagnifolium clade, subgenus Leptostemonum. The Solanaceae family consists of about 102 accepted genera, about 2,878 accepted species, and 3,258 intraspecifics worldwide, according to the Plants of the World Online (POWO) database of the Royal Botanic Gardens, Kew. The Solanaceae family has a cosmopolitan distribution from tropical to subtropical to temperate regions worldwide, with high concentrations in the Americas. The genus *Solanum* of the Solanaceae family is approximately 1,242 widely recognized species found throughout the world (POWO 2025). *Solanum* is considered one of the ten most species-rich angiosperm genera with a wide distribution in temperate and tropical parts of the world (Knapp et al. 2017). In the Gaza Strip, Palestine (Table 3), *S. elaeagnifolium*, *S. nigrum*, *S. villosum*, *S. pilcomayense, S. tuberosum*, etc. are common (Abou Auda and Ighbareyeh 2024).

Figure 2. Morphological appearance of *Solanum elaeagnifolium* under different environmental conditions. A. Plant growth under optimal conditions in undisturbed habitat; B-D. Plants observed under harsh, stressful conditions and degraded habitats, including drought, poor soils, and anthropogenically disturbed sites in the Gaza Strip, Palestine (Photo: Qassem Ramiz Abed Rahman, 17.05.2025, Maghazi Area, Gaza Strip)

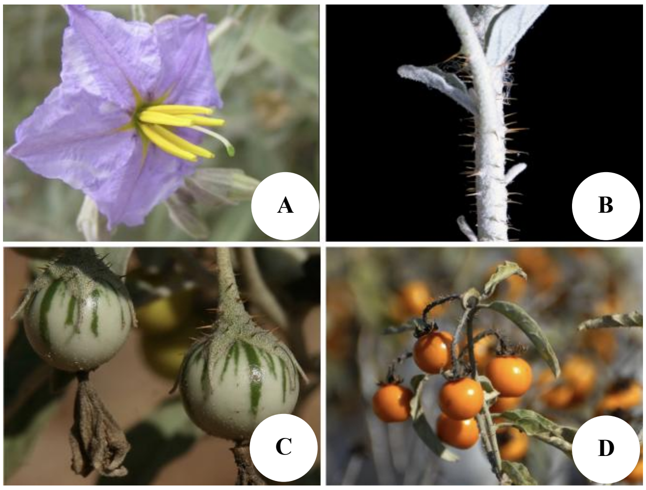

Figure 3. A. The detailed flower structure of *S. elaeagnifolium* is typically 5-merous and perfect. The reflexed blue corolla encloses five equal, banana-shaped anthers; B. Stems and leaves are covered with dense star-shaped trichomes on almost all surfaces. Leaves are simple or slightly lobed, elliptic to lanceolate, with the adaxial leaf surface darker green than the abaxial; C. Young fruit; D. The mature berry is globose, smooth, and glabrous, transitioning from yellow to orange as it ripens. Upon full maturity, it dehisces to reveal an orange to brown interior. It contains numerous flattened seeds that are orange brown in color and tend to detach in a mass when the fruit splits open (Danin and Fragman-Sapir 2016)

Table 1. Morphological and ecological traits of *Solanum elaeagnifolium* (Qasem et al. 2019)

Trait	Observation
Life form (Raunkiaer)	Hemicryptophyte-overwintering buds at soil surface level
Spinescence	Emergences-prickles (in unexpected places)
Succulence	Non-succulent
Summer shedding	Ephemeral (shed aerial parts during summer stress)
Flower color	Lilac with yellow stamens
Reproductive morphology	Flowers hermaphrodite only
Seed homogeneity	Homogeneous seeds-fruits
Leaf arrangement	Alternate (one leaf per node)
Leaf type	Entire
Leaf margin	Smooth
Stipule	Absent
Habitat	Cultivated areas (weeds)
Drought resistance	Moderate
Salt resistance	Glycophyte
Synanthropy	Obligate synanthropic

Global vernacular names

Wherever *S. elaeagnifolium* occurs as an invasive plant, it is known locally as silverleaf nightshade (Wu et al. 2016). In the United States, the plant also goes by various names such as silverleaf nightshade, tomato nightshade, white horsenettle, trompillo, and white nightshade (Knapp et al. 2017). *Solanum elaeagnifolium* is found in northern Mexico and the southwestern United States (Tataridas et al. 2023). A taxonomic revision of the group was presented by Knapp et al. (2017). It is locally called al-sajwa al-zaytiya or badenjan barri in the Gaza Strip, Palestine (Abou Auda 2025a). It is known worldwide by a number of vernacular names, including white horsenettle, bullnettle, tomatillo, meloncillo, and trompillo (Kwong et al. 2006). Its epithet, elaeagnifolium, is due to its silvery leaves, which resemble those of Elaeagnus species. In South Africa, it is known by the common names "silverleaf bitter apple" or Satansbos, as it is a known invader (Wilson et al. 2013). In South Korea, its local name, Eun-bit-kka-ma-jung, emphasizes its silvery appearance with a local popular plant (Hong et al. 2014). Among Algerian farmers, it is known as echouka (thorn) due to its spiny stems (Adjim and Kazi-Tani 2018). In Greece, this plant is commonly referred to as the 'Lernaean Hydra' due to its aggressive regrowth after herbicide application (Krigas et al. 2021). These diverse vernacular names reflect not only the widespread occurrence of *S. elaeagnifolium* but also local ecological knowledge and perceptions of its invasive behavior and toxicity, underscoring the need for community-engaged management in infested regions.

Distribution in the Middle East

Solanum elaeagnifolium, native to the southern regions of North America, is now one of the most aggressive and damaging invasive species in many Mediterranean countries and poses a major ecological and agricultural problem (Roberts and Florentine 2022; Balah and Hassany 2023). However, it has become a widespread and problematic invader across Mediterranean climates, including the Middle East, southern Europe, and Australia. In its native range, the species typically occurs in disturbed habitats such as roadsides, pastures, and open shrublands, where it coexists with native flora under natural checks by herbivores and pathogens. In contrast, in invaded regions like the Gaza Strip, *S. elaeagnifolium* forms dense monocultures, often displacing native vegetation and reducing biodiversity. Studies from Mediterranean Europe have reported significantly higher seed production, increased root biomass, and greater drought tolerance in invasive populations compared to native ones, indicating strong adaptive plasticity. Additionally, in the Gaza Strip, its spread is facilitated by overgrazing, poor soil structure, and the absence of natural enemies, allowing it to dominate fallow lands, olive orchards, and disturbed urban peripheries. The success of *S. elaeagnifolium* in such environments is likely due to its high phenotypic plasticity, tolerance to drought, and lack of natural enemies, common features of successful invaders. Its seed dormancy, allelopathic traits, and deep rhizome system contribute to persistence even under intermittent control efforts. In Syria, it is one of the most widespread invasive species, and it is estimated that 60% of arable land is infested. In Iraq, the weed has also spread rapidly, with infested areas reported to have reached 148 hectares in 2014. In Jordan, the weed was found on around 43 hectares, while in Lebanon it continues to be limited with an infestation of less than 1 hectare (Chiarini et al. 2018; Tataridas et al. 2023). Field records and herbarium collections confirm the occurrence of non-cultivated *S. elaeagnifolium* populations in Egypt, Iraq, Jordan, Kuwait, Saudi Arabia, and Palestine (Knapp et al. 2017).

A visual summary of the plant's native and introduced geographical range is illustrated in Figure 4, showing its origin in the Americas and invasive spread across the Middle East and other regions. The plant thrives on roadsides, croplands, and disturbed habitats and tends to form dense stands that are difficult to control due to its deep root system and high seed production.

Given the ongoing war and humanitarian crisis in the Gaza Strip, Palestine, access to many regions remains highly restricted and dangerous, limiting the ability of local researchers to conduct field-based ecological surveys or collect high-resolution distribution data on *S. elaeagnifolium*. Nevertheless, preliminary observations indicate rapid dispersal in disturbed habitats. To address the current gap in predictive modeling and ecological risk assessment, future studies should integrate satellite imagery, field surveys, and environmental factors (e.g., grazing pressure, land degradation, and land abandonment) to develop risk maps and model dispersal dynamics. The invasion of *S. elaeagnifolium* is likely to disrupt key ecosystem services such as soil fertility, pollinator interactions, and agricultural productivity, posing a serious threat to biodiversity and traditional farming systems. Post-conflict ecological monitoring and regional collaboration will be essential to mitigate its impact and inform effective management strategies.

GLOBAL INVASIVE WEED THREATENING AGRICULTURE, LIVESTOCK, AND ECOSYSTEMS

Solanum elaeagnifolium is recognized worldwide as a highly invasive and noxious weed with severe impacts on agricultural productivity, animal health, and ecosystem stability (Tataridas et al. 2022b). *Solanum elaeagnifolium* has been translocated from North America to other continents, particularly in arid regions. It infests pastures and poor-quality croplands, posing a threat as its content of solasodine deters grazing. Its invasive nature is made possible by excessive seed production and deep roots that make control difficult. It is legally established as a noxious weed in most nations (Hong et al. 2014). Its spread has been documented in several Mediterranean and Middle Eastern countries, with significant economic impacts. Jordanian bell pepper growers reported high management costs and significant yield losses due to successive re-spreading (Qasem 2014).

In Greece, competition with this weed reduced alfalfa yields by 8-26% (Travlos 2013). In Tunisia, it affected over 2,300 hectares of irrigated land and seriously impacted summer crops (Sayari and Mekki 2021). Egyptian barley yields also fell by 30% in infested fields (Amer 2021). *Solanum elaeagnifolium* not only competes with crops but also serves as a host for a variety of pests and diseases that destroy crops. It is also responsible for the spread of the parasitic weed *Orobanche ramosa* in tomato fields (Qasem et al. 2019) and harbors viruses such as cucumber mosaic virus, tomato yellow leaf curl virus, and pepper mild mottle virus (Zammouri and Mnari-Hattab 2014).

The plant also releases chemicals that affect the growth of important crops such as wheat and cotton (Balah and Abdel-Razek 2020). In addition to being a threat to crops, *S. elaeagnifolium* is also highly toxic to cattle and poses a threat, albeit to a lesser extent, to rabbits, sheep, and goats (Qasem 2014), further reinforcing its reputation as a serious agricultural and ecological problem. These impacts align with traits typically associated with invasive success, including prolific seed output, rapid vegetative reproduction, and strong chemical defenses. Its role as a viral and parasitic weed host adds an indirect layer of damage by facilitating crop disease outbreaks.

One mechanism that helps explain the ecological dominance of *S. elaeagnifolium* is its allelopathic potential underpinning the ecological success of invasive plants like *S. elaeagnifolium*. According to recent reviews and empirical studies, allelopathy can directly inhibit seed germination, seedling establishment, and biomass accumulation of neighboring species through the release of phytotoxic compounds into the environment via leaf leachates, root exudates, and decaying plant material (Akbar et al. 2024). The aqueous extract of *S. elaeagnifolium* showed a species-specific allelopathic effect on seed germination and seedling growth. The most susceptible germination EC_{50} was observed in *Polypogon monspeliensis* (1.99±0.29 g DW-100 mL^{-1}), followed by *Phalaris minor* (2.33±0.19) and *Allium cepa* (2.57±0.01). *Zea mays* and *Portulaca oleracea* had the highest EC_{50} values for germination at 5.88±0.29 and 5.25±0.32, respectively. For vegetative growth, the EC_{50} values for root length were lowest for *P. monspeliensis* (1.55±0.13) and *P. minor* (2.15±0.22), indicating higher sensitivity, while *Z. mays* (4.29±0.45) and *Vicia faba* (5.71±0.59) were more tolerant. The EC_{50} values for shoot length were comparable, with *P. minor* and *P. monspeliensis* showing strong inhibition (2.01±0.13 and 1.89±0.19, respectively) and *Z. mays* and *V. faba* showing values above 4.6. These results confirm that *S. elaeagnifolium* exerts a strong inhibitory effect, especially on root growth, with monocotyledonous weeds generally being more susceptible (Balah et al. 2022).

Of particular interest in this context are phenolic acids, flavonoids, terpenes and steroidal glycoalkaloids, the allelochemicals extracted from *S. elaeagnifolium*, most of which have a significant inhibitory effect on the germination and growth of crops and native plants. This activity is often dose-dependent, species-specific and sustained under different soil and water regimes (Antodiadis et al. 2024).

ECOLOGICAL IMPACT AND INVASION POTENTIAL OF *S. elaeagnifolium* IN MEDITERRANEAN AND GAZA STRIP HABITATS

The Mediterranean Basin is internationally recognized as a biodiversity hotspot due to its exceptional levels of plant endemism and ecological richness (Pires et al. 2024). However, this fragile biodiversity is increasingly threatened by invasive alien species such as *S. elaeagnifolium*, which exhibit aggressive expansion in disturbed and semi-natural habitats (Syngkli et al. 2025). Although comprehensive assessments of its ecological impacts remain limited, available studies reveal that *S. elaeagnifolium* can establish dense monospecific stands, particularly in degraded or overgrazed areas, leading to substantial declines in native plant diversity. As reported by Balah and Hassany (2023), floristic analyses indicate severe biodiversity impacts: in invaded sites of Borg al-arab and El-hammam (analogous to Gaza's agroecosystems), *S. elaeagnifolium* dominates 25-37% of cultivated lands, reducing native species richness by 9-18% compared to non-invaded controls (33 vs. 30 species in Borg al-arab; 30 vs. 27 in El-hammam).

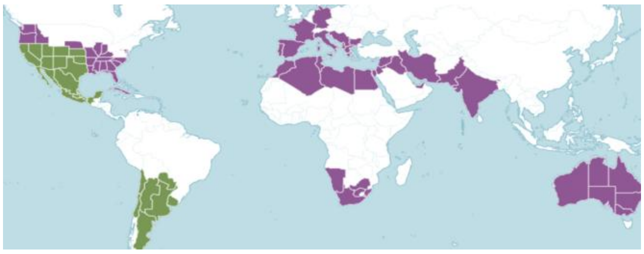

Figure 4. Global geographical distribution map of *Solanum elaeagnifolium.* Green areas represent regions where the species is native, such as in parts of North and South America. Purple areas show regions where the species has been introduced, particularly in the Middle East (POWO 2025)

Seasonal data show greater suppression in summer (14 species surviving vs. 19 in winter), with Poaceae and Brassicaceae most vulnerable. The invader achieves Relative Abundances (RA) of 19.97-30.81, surpassing even resilient natives like *Silybum marianum* (RA:18.14) and *Cynodon dactylon* (RA:18.56). Its summer dominance peaks at RA:59.04, displacing key species like *Dactyloctenium aegyptium* (RA:23.84) that stabilize soils in Gaza's wadi systems. For instance, *S. elaeagnifolium* invasion has been associated with reduced pollinator visitation and lower seed set in native flora, suggesting disruption to plant-pollinator networks and reproductive success (Sayari et al. 2022). These findings suggest that *S. elaeagnifolium* not only competes for space and resources but may also disrupt ecological networks, affecting mutualistic interactions such as pollination and seed dispersal (Table 2). Similarly, its presence as the only exotic species in disturbed soils of a forest restoration site in Northern Greece reflects its competitive dominance and ability to exclude other colonizers (Uludag et al. 2016). In ecosystems subjected to low-intensity grazing, common in Mediterranean pastoral systems, the species often becomes dominant over time, suppressing forage diversity and indirectly affecting higher trophic levels, including native herbivores, granivorous birds, and insectivorous fauna. Moreover, due to its extensive rhizome system and allelopathic potential, *S. elaeagnifolium* can alter soil chemistry and nutrient cycling, further hindering the reestablishment of native vegetation (Balah et al. 2022). As shown in Table 2, these cumulative impacts not only reduce biodiversity but may also impair key ecosystem functions such as pollination, seed dispersal, and soil stabilization. As such, its spread poses a multidimensional ecological threat across Mediterranean-type ecosystems globally. Ecological conditions in the five governorates of Gaza strip (Gaza City, North Gaza, Khan Yunis, Rafah, and Deir Al-Balah) are consistent with habitat types commonly invaded by *S. elaeagnifolium* in semi-arid regions (Uludag et al. 2016; Qasem et al. 2019; Kobisi et al. 2024). *Solanum elaeagnifolium* is a highly invasive perennial weed whose success is driven by rapid growth, phenotypic plasticity, and allelopathic effects. The species exhibits peak germination in spring (63.5-63.8% in March-April), declining sharply in winter (6.3% in December-January), and progresses through five life stages—seedling, juvenile, flowering, fruiting, and seed dispersal completing its lifecycle in 40-90 days (Balah and Hassany 2023). Key physiological adaptations include an increasing shoot-to-root ratio (0.86 to 1.70 g g^{-1}) and dynamic resource allocation, favoring leaf mass over root biomass as it matures. Invaded communities show reduced biodiversity, with lower Simpson (λ: 0.023-0.06 vs. 0.028-0.07 in non-invaded) and Shannon indices (H': 2.605-2.894 vs. 2.625-3.055), reflecting dominance by *S. elaeagnifolium* (Balah and Hassany 2023). Additionally, the weed alters soil biochemistry, increasing phenolic content by 40% and reducing mycorrhizal colonization by 2.3×, which further suppresses native plant establishment (Karmezi et al. 2023). These traits collectively enhance its invasiveness, enabling colonization across agricultural and disturbed habitats.

INTEGRATION OF ECOLOGICAL TRAITS AND PHYTOCHEMICAL COMPOSITION

The spread and invasiveness of *S. elaeagnifolium* are intricately tied to its ecological traits, particularly its adaptability to stressful environments. Its drought tolerance and ability to regenerate from rhizomes make it a formidable invasive species in arid and semi-arid regions like the Gaza Strip (Sayari et al. 2022). This resilience under harsh conditions may influence its phytochemical composition, potentially enhancing the concentration of secondary metabolites such as flavonoids, glycoalkaloids, and terpenoids (Kumar and Singh 2020). For instance, drought-stressed plants often increase their production of antioxidants, like quercetin and kaempferol, as part of their stress defense mechanisms, which protect them from oxidative damage (Gowtham et al. 2022). Moreover, the invasive nature of this plant means that as it spreads across disturbed lands, it could become a major source of bioactive compounds for local populations who may lack access to conventional healthcare resources. Phytochemical research on *S. elaeagnifolium* indicates that its bioactive properties, such as antioxidant and anti-inflammatory activities, are already well-documented, suggesting the potential of utilizing this plant for pharmaceutical applications (Bouslamti et al. 2022b; Al-Hamaideh 2023; Almatroodi et al. 2024). As the plant invades new territories, such as abandoned agricultural lands in the Gaza Strip, it could provide local populations with alternative sources of medicine, especially in conflict zones where pharmaceutical access is limited.

Table 2. Habitat conditions in Gaza Strip, comparable to disturbed sites typically invaded by *Solanum elaeagnifolium* (Uludag et al. 2016; Qasem et al. 2019; Kobisi et al. 2024)

Site name	Habitat type	Soil texture	Vegetation cover	Disturbance type
Gaza City	Abandoned field	Sandy loam	Sparse	Agricultural neglect
North Gaza	Roadside	Clay loam	Moderate	Urban disturbance
Khan Yunis	Pasture	Sandy	Patchy	Grazing and trampling
Rafah	Abandoned/fallow field near dune margins	Loessial sandy clay loam over dune sand	Sparse to patchy (low shrubs and weeds)	Agricultural abandonment, grazing, urban edges
Deir Al-Balah	Wadi edge and light-slope orchard zone	Sandy loam (calcareous, wadi deposits)	Patchy (shrubs and annuals)	Wadi flooding, orchard cultivation, grazing

The ecological spread of *S. elaeagnifolium* also brings challenges. Its invasive success diminishes biodiversity, potentially reducing the availability of other medicinal plants and food crops. Invasive species like *S. elaeagnifolium* often alter ecosystem, soil fertility and pollinator networks, which could, in turn, affect the future availability of natural bioresources (Karmezi et al. 2023). However, this plant's dual nature, both as a threat and a potential resource, illustrates the paradox inherent in many invasive species, making *S. elaeagnifolium* a complex but important subject for ongoing research into medicinal applications and ecological management.

BENEFICIAL TRADITIONAL USES AND POTENTIAL INDUSTRIAL APPLICATIONS

To enhance synthesis and accessibility, this section summarizes the key traditional uses, cultural significance, and potential industrial applications of *S. elaeagnifolium*, while also identifying knowledge gaps relevant to the Gaza Strip. Wild plant species are an indispensable component of natural biodiversity and represent essential resources for food and traditional medicine, particularly for rural and resource-poor communities, in the face of increasing food insecurity worldwide (Ullah et al. 2023). In addition to their subsistence value, these species also hold significant economic and industrial importance, as they provide raw materials for the chemical, food, cosmetic, pharmaceutical, and agricultural industries (Karagozoglu and Kıran 2023).

Phytochemical analyses have demonstrated that the diverse secondary metabolites and mineral elements present in wild plants can significantly impact human metabolic functions. Various parts of plants, including leaves, seeds, flowers, bark, roots, fruits and, in some cases, the whole plant, are traditionally harvested and used for their therapeutic or nutritional properties (Tripathi et al. 2023). Worldwide, wild forage plants play a crucial role in animal feed, serving as the primary feed component in smallholder and pastoral production systems (Geng et al. 2020).

Forage selection per species is usually based on nutrient content, palatability, and seasonal variation. Therefore, a proper understanding of their nutritional value is necessary not only to increase livestock production but also to maintain native herbivorous wildlife and balance in ecosystems (Geng et al. 2020). Despite its harmful effects, *S. elaeagnifolium* has been discovered to have numerous potentials uses in agriculture, medicine, industry, and nutrition. Historically, the Pima Indians consumed the ripe fruit as a natural milk coagulant (Néstor et al. 2012). There is also an industrial use of seed oil for biofuel production, as well as for the manufacture of shampoo and soap (Feki et al. 2013). It has also been successfully crossed with eggplant (*S. melongena*) in agricultural breeding, producing drought- and nitrogen-tolerant lines (Villanueva et al. 2021).

Solanum elaeagnifolium is also a trap crop for the parasite *O. ramosa*; however, caution is advised if the tomato is successful in the rotation (Qasem et al. 2019). Phytochemical analyses have revealed a high content of phenols and flavonoids, particularly in the seeds, which exhibit a strong antioxidant effect (Feki et al. 2014). They are also responsible for antiglycation and protect against diabetic complications such as arteriosclerosis and cataracts (Houda et al. 2014). Leaf extracts have an inhibitory effect on human pathogens (Balavivekananthan et al. 2021), and certain compounds are naturally anticancer (Hernandez et al. 2017). In animal husbandry, although consumption by ruminants is generally avoided due to the presence of tannins and poor digestibility, pre-flowering grazing by goats on dry soils can increase nutrient uptake and prevent the spread of weed seeds (Mellado et al. 2008). These multifaceted applications are particularly relevant for marginalized areas such as the Gaza Strip, where alternative bioresources could contribute to local resilience and innovation in green industries.

The conventional preparation of *Solanum* components typically involves pureeing fresh plant material for use in poultices, preparing decoctions for consumption or washing, or sometimes infusing plant components in oil. The choice of plant components intended for use (leaves, fruits, or roots), the degree of ripeness, and the method of preparation are crucial parameters that traditional practitioners usually obtain through experimental experience passed down across generations. These data are of crucial importance for therapeutic optimization to avoid potential toxicity from toxic ingredients, such as glycoalkaloids.

Despite promising findings, several bioactivity claims remain insufficiently validated, particularly regarding dosage, toxicity thresholds, and potential side effects in humans. Moreover, region-specific ethnobotanical studies should assess both pharmacological promise and potential toxicity under local usage patterns, particularly where regulation of herbal preparations is lacking. Many studies are limited to in vitro or animal models, with few progressing to preclinical or clinical trials. Glycoalkaloids, for example, show anticancer and antimicrobial activity, but also pose toxicological concerns at high concentrations. Thus, future pharmacological studies should prioritize dose-response assessments, safety profiling, and clinical relevance. Tables 7 and 8 provide a structured overview of the main compounds and their reported biological targets. The socio-cultural importance of these plants in Gaza goes beyond their medicinal use. Time-sensitive documentation is vital, especially in conflict zones like Gaza, where traditional plant knowledge is at risk of disappearing due to population displacement and generational gaps. They are part of the region's ecology, and information about them contributes to the autonomy of healthcare and the resilience of society. However, as with most traditional information systems, there is a risk of erosion due to modernization processes and changing lifestyles. Scientific documentation and certification of these ethnobotanical applications are necessary not only to preserve cultural heritage but also to identify potential new sources of therapeutic agents that may be of particular importance in contexts such as the Gaza Strip, where access to conventional medicine may be limited. It is highly advisable to conduct more systematic ethnobotanical surveys, particularly in the Gaza Strip, to systematically document local knowledge of *Solanum* species, their use, preparation, and perceived efficacy and safety. Such research would be extremely valuable in bridging the gap between traditional and modern scientific knowledge, benefiting local communities, and advancing scientific progress in general. Proper ethnopharmacological validation protocols, including community interviews and herbalist consultations, are recommended to ensure safety and respect for indigenous knowledge systems in future research.

NUTRITIONAL COMPOSITION OF *S. elaeagnifolium*

Current proximate analysis that was conducted on *S. elaeagnifolium* collected from the Gaza Strip has validated its rich nutritional value and its use as a functional phototherapeutic product (Table 4). The leaves and flowers of the plant recorded high content of crude fibers and carbohydrates, hence rich in calories (approximately 365-368 kcal/100g).

The leaves contained a combined total of 14.1% proteins and 2.26% nitrogen and reflected considerable amino acid content, while the flowers reflected slightly lower values. The plant further reflected considerable amounts of potassium (2.6-3.3%) and phosphorus (0.21-0.24%), essential minerals that enhance cardiovascular and metabolic states (Abou Auda 20205a). Such a biochemical nature confirms earlier claims regarding its antioxidant and hepatoprotective activities as postulated in various studies. Apart from this, its ethno-medicinal application traditionally and high fiber content suggest its possibility to manage digestive disorders, lipid metabolism, and oxidative stress. However, the presence of bioactive secondary metabolites also necessitates proper handling, particularly its livestock toxicity, as mentioned in ethnobotanical records in concomitant arid ecosystems (Abou Auda 20205a). However, while the nutritional benefits are promising, it is crucial to standardize intake recommendations and identify any thresholds for adverse effects, particularly for vulnerable populations such as children, the elderly, or those with metabolic disorders.

PHARMACOLOGICAL AND TOXICOLOGICAL PROFILE

Mechanisms of toxicity

Plants produce a wide range of bioactive secondary metabolites as defense mechanisms against herbivores, pathogens, and abiotic stress (Divekar et al. 2022). These metabolites include neurotoxins, hepatic, and renal toxins, cytotoxins, and metabolic inhibitors that disrupt fundamental biological processes in target organisms (Ibrahim et al. 2018). These toxins gave plants the impetus to survive under extreme conditions and enabled the use of plant material in medicine throughout history (Ibrahim et al. 2021).

Hepatotoxic, nephrotoxic, and neurobehavioral effects

Neuroprotective strategies highlight the importance of using effective, affordable natural antioxidants to help maintain the balance between oxidants and cellular antioxidants, thereby protecting the central nervous system from oxidative stress, neurodegeneration, and cell death (Eleyan et al. 2018b).

Treatment with a high dose (2000 mg/kg) of hydroethanolic *S. elaeagnifolium* fruit extract resulted in multiorgan toxicity. Significantly high alanine aminotransferase (ALT), aspartate aminotransferase (AST), and alkaline phosphatase (ALP) levels indicated hepatocellular damage, supported by a slight infiltration of the liver tissue with inflammatory cells without necrosis. Renal toxicity was indicated by high bilirubin and creatinine levels and histologic evidence of glomerular cell loss and enlargement of Bowman's space, with tubules intact.

Table 3. *Solanum* species in the Gaza Strip, Palestine, botanical features, and primary traditional uses (Abou Auda 2012, 2025b)

Species name	Common names	Botanical features	Primary traditional uses in the Gaza Strip, Palestine
S. nigrum	Black nightshade, Enab Al-Deeb	Annual/short-lived perennial herb; ovate leaves; small, white, star-shaped flowers; ripe berries purplish-black	Leaves (boiled) for skin conditions (boils, burns, eczema), fevers, headaches; diuretic, laxative. (Unripe berries toxic; use with knowledge)
S. elaeagnifolium	Silverleaf nightshade	Perennial herb/subshrub; silvery-grey foliage (stellate trichomes); violet/blue flowers; yellow/orange-brown ripe berries	Limited specific Gazan uses documented; other regions: skin diseases, analgesic (Invasive, potentially toxic to livestock)
S. pilcomayense	Pilcomayo nightshade	Erect, often subshrubby *Solanum* with prickles; similar leaf morphology to *S. elaeagnifolium*; native to South America but found in arid zones	considered toxic or weedy; suspected to have glycoalkaloids similar to other *Solanum* spp. (Requires further ethnobotanical study)
S. villosum	Hairy nightshade, Red-berried nightshade	Annual/biennial herb; densely hairy; white flowers; ripe berries orange/yellow-red	Similar uses to *S. nigrum*; ripe berries sometimes consumed (Distinguish from more toxic species; unripe parts)

Table 4. Proximate composition of *Solanum elaeagnifolium* (leaves and flowers) in the Gaza Strip, Palestine (Abou Auda 20205a)

Parameter	Leaves (%)	Flowers (%)
Moisture content	4.5	7.1
Crude fiber	32.4	27.9
Total proteins	14.1	13.4
Total carbohydrates	70.3	72.2
Ash content	12.5	11.5
Total lipids	3.1	2.9
Nitrogen	2.26	2.14
Potassium	2.6	3.3
Phosphorus	0.21	0.24
Energy value (Kcal/100g)	365.14	368.39

Neurological effects such as lethargy, convulsions, anorexia, and death within 12 hours reflect the effects on the systemic and central nervous systems at toxic doses (Bouslamti et al. 2024). In arid regions such as Gaza Strip, where traditional plant use remains prevalent, such toxicity profiles underscore the need for community awareness campaigns and labeling guidelines to prevent unintentional poisonings, especially when plant parts are used as folk remedies.

All toxicological studies referenced were conducted according to internationally accepted ethical standards for animal research, including humane endpoints and ethical approval protocols as reported in the original studies (e.g., Bouslamti et al. 2024). Nevertheless, additional transparency in future research is needed to ensure full compliance with the 3Rs principle (Replacement, Reduction, Refinement) in animal testing. Furthermore, future in vivo studies should adopt region-specific strains and dietary models to improve translatability of toxic effects in endemic populations.

Molecular basis of toxicity

Solasodine, a steroidal alkaloid, is widely known as the main aglycone (non-sugar moiety) of most glycoalkaloid-containing *Solanum* species (Zhao et al. 2023). It serves as the core structure for the formation of several biologically active glycoalkaloids. Among these, the water-soluble triglycosides solasonine (SN) and solamargine (SM) are particularly widespread and have been identified in over 200 species of the genus *Solanum* (Al Sinani and Eltayeb 2017; Zeng et al. 2022). These compounds usually consist of solasodine bound to sugar residues such as rhamnose, glucose and galactose and are known for their cytotoxic, antifungal, and anticancer properties (Zhao et al. 2024). Their concentration and bioactivity often vary depending on the plant organ (e.g., roots, leaves, fruits) and developmental stage, and they are among the primary defense-related secondary metabolites in *Solanum* plants. Comparative analysis across arid-region populations suggests that glycoalkaloid levels may be modulated by climatic stress, offering an ecological explanation for phytochemical variability (Zeng et al. 2022). The dual presence of SN and SM in many species underlines their evolutionary and pharmacological importance, especially in the context of membrane disruption and induction of apoptosis in malignant cells (Al Sinani and Eltayeb 2017).

β-Solamine, a bioactive steroidal glycoalkaloid isolated from the seeds, is very active and has molluscicidal potential (LC50: 0.49 mg/L). Its strong biological activity may form the basis for neurotoxicity and membrane-disrupting mechanisms also in mammals. Steroidal alkaloids such as solamargine and solasodine can bind to cholesterol in membranes and impair mitochondrial and lysosomal integrity, a common toxic mechanism for glycoalkaloids (Bekkouche et al. 2000). These compounds may also offer chemotaxonomic markers distinguishing *S. elaeagnifolium* from other invasive *Solanum* species, a concept proposed in phytochemical studies across Mediterranean and African biomes (Akbar et al. 2024). This aligns with recent findings that allelopathic and antimicrobial effects of *S. elaeagnifolium* may share a mechanistic basis with its toxicity in vertebrates, reinforcing the idea of dual-purpose secondary metabolites (Balah et al. 2022).

The toxicological profiles (Table 5) of the different extracts indicate hepatotoxicity, nephrotoxicity, and hematotoxicity, which are severe at higher doses, particularly for the seed and fruit components. Mechanisms include oxidative damage, membrane disruption, and inflammatory reactions, so caution is advised in therapeutic use. These findings stress the importance of dosage control and standardization if plant-based therapeutic formulations are to be developed from *S. elaeagnifolium*.

In experimental studies, *S. elaeagnifolium* has demonstrated hepatoprotective effects comparable to those of silymarin, a well-established liver-protective agent. Administration of *S. elaeagnifolium* extract at appropriate doses led to the normalization of liver enzyme markers ALT, AST, and ALP in animal models subjected to paracetamol-induced hepatotoxicity. Unlike the high-dose toxicity observed in other contexts, this hepatoprotective effect occurred without any signs of systemic or hepatic toxicity, suggesting a favorable safety profile at therapeutic levels (Hawas et al. 2013). These dual pharmacological profiles reflect a common pattern in medicinal plants where beneficial and harmful outcomes depend on dose, extraction solvent, and route of administration (Hernandez et al. 2017).

Although these findings are derived from animal models, they offer preliminary indications of potential human toxicities, particularly at high doses. Translational relevance requires cautious extrapolation, as metabolic, physiological, and dose-response differences between species may affect human safety profiles. In future Gaza-based applications, regionally tailored pharmacokinetic models using local dietary and exposure data would greatly enhance predictive safety evaluations. Therefore, bridging studies, including pharmacokinetic and pharmacodynamic modeling, are crucial to determine human applicability.

Table 5. Toxicological and hepatoprotective effects of *Solanum elaeagnifolium* (Bouslamti et al. 2024)

Parameter	Treatment/Dose (mg/kg)	Key findings	Toxic effects	Significance
Liver function	Leaf extract (≤1000)	Mild, dose-independent ALT/AST elevation	None	Non-toxic at ≤1000 mg/kg
Liver function	Fruit extract (2000)	Significant ALT/AST increase ($p<0.001$)	Hepatotoxic	Toxic at high doses
Kidney function	Fruit extract (2000)	Elevated creatinine ($p<0.01$)	Potential nephrotoxicity	High-dose toxicity risk
Hematological effects	Fruit extract (2000)	Reduced RBCs, elevated HGB/HCT ($p<0.001$)	Possible alterations in erythropoiesis	Blood-related toxicity
Acute oral toxicity	500 (Leaf/Fruit)	No mortality	None	Considered safe
Acute oral toxicity	1000 (Fruit)	No mortality	Mild symptoms	Moderate safety profile
Acute oral toxicity	2000 (Leaf)	1/5 mortality	Severe, delayed toxicity	Not recommended
Acute oral toxicity	2000 (Fruit)	2/5 mortality	Convulsions, lethargy	Highly toxic

Despite its demonstrated bioactivities, the therapeutic window and safety margin of *S. elaeagnifolium* remain insufficiently defined. However, the pharmacological exploration of *S. elaeagnifolium* is tempered by significant safety concerns and translational hurdles. In particular, the plant's steroidal glycoalkaloids, solanine, solamargine, and solasonine, are well-documented toxins that demand caution (Choon and Khiruddin 2025). Solanine and solamargine can trigger severe gastrointestinal and neurological disturbances along with cardiac effects (Al Sinani and Eltayeb 2017; Ziemke et al. 2024). These glycoalkaloids share a disruptive mechanism of action, binding to membrane cholesterol and damaging cellular organelles, which underlies their potent cytotoxic and neurotoxic effects (Bhambhani et al. 2021). Toxicological studies in animals confirm a narrow safety margin, high-dose extracts (e.g., ≥2000 mg/kg) induce multiorgan toxicity and neurological symptoms. The lower doses (≤1000 mg/kg) are far better tolerated (Bouslamti et al. 2024). This dose-dependent risk highlights the critical need for strict dosage control and standardization if any therapeutic use is pursued. Equally important, there is a paucity of human pharmacokinetic and clinical data on these compounds, so current safety assumptions rely on in vitro and animal models. Such experimental systems cannot fully replicate human metabolism and sensitivity, meaning toxicokinetic profiles and safe exposure thresholds in humans remain undefined. These gaps underscore an urgent need for rigorous preclinical validation and translational pharmacology studies. Future investigations must prioritize comprehensive safety profiling, including detailed dose-response evaluations, chronic toxicity assays, and pharmacokinetic analyses, before any human trials are considered. Bridging this translational gap will be essential to establish human-relevant dosage guidelines and to ensure that any prospective therapeutic applications of *S. elaeagnifolium* are both efficacious and safe.

MOLECULAR PHARMACOLOGY

Bioactive terpenoids and pharmacological significance

Terpenoids are a large class of oxygenated secondary metabolites composed of isoprene units that are characterized by their volatility and aromaticity and form an important component of essential oils (Siddiqui et al. 2024). Monoterpenes, sesquiterpenes, diterpenes, and triterpenes are some of the molecules that are biosynthesized via the mevalonate and methyl erythritol phosphate pathways (Ashour et al. 2010; Perez-Gil et al. 2024). They play various ecological roles in plants, particularly in stress responses, and are known for their therapeutic applications in antimicrobial, anticancer, anti-inflammatory, and antiviral treatments (Dhifi et al. 2016).

In *S. elaeagnifolium*, gas chromatography of leaf extracts identified a number of bioactive terpenoids, including (E)-caryophyllene, (Z)-jasmone, and geranyl-linalool isomers (Tsaballa et al. 2015). These sesquiterpenes and diterpene alcohols are known for their antimicrobial (Espinoza et al. 2019), anti-inflammatory (Wu et al. 2022), and cytoprotective properties (Khanam et al. 2025).

(E)-caryophyllene, for example, is an analgesic and anti-inflammatory bicyclic CB2 receptor sesquiterpene (Dickson et al. 2023). Similarly, (Z)-jasmone plays a role in defense signaling and scenting the plant (Schuman et al. 2018), and isomers of geranyl linalool may possess insect repellent and antimicrobial properties (Fajdek-Bieda et al. 2024). The presence of such compounds confirms its pharmacological potential and warrants further investigation into the profile and bioactivity of the essential oil. These compounds may also contribute to allelopathic interactions with competing vegetation in arid ecosystems, enhancing the plant's invasive potential, an effect observed in Mediterranean analogs (Espinoza et al. 2019).

Pharmacological roles of tannins

Tannins are polyphenolic compounds that are widely distributed in land plants, including *S. elaeagnifolium*, and are predominantly found in leaves, fruits, and seeds (Feki et al. 2014; Bouslamti et al. 2022a). Tannins have been used as feed additives in animal production for centuries due to their effects on the gut microbiota and metabolism (Fonseca et al. 2023). Tannins can increase feeding efficiency, improve animal welfare, and influence meat quality when used in appropriate concentrations (Besharati et al. 2022). Biologically, tannins are both beneficial and detrimental, depending on their structure, dosage, and host physiology (Piluzza et al. 2014). In addition to their nutritional effects, tannins are also recognized to exhibit antioxidant (Baldwin and Booth 2022), antimicrobial (Maisetta et al. 2019), and anti-inflammatory properties (Squillaro et al. 2018), as they are able to chelate metals (Truong and Jeong 2021), scavenge free radicals, and bind microbial enzymes (Ke et al. 2022). In pharmacological screening of *S. elaeagnifolium*, tannins have also been associated with membrane stabilization and antimicrobial activity, contributing to the plant's therapeutic profile (Farha et al. 2020). Moreover, their astringent and metal-chelating actions may also interfere with nutrient availability for co-occurring plant species, offering a mechanistic clue to their allelopathic roles in disturbed Gaza environments.

Bioactive saponins: Structure, distribution, and bioactivity

Saponins are a class of naturally occurring glycosides widely distributed throughout the plant kingdom, characterized by their ability to form soap-like foams when shaken in aqueous solutions (Vincken et al. 2007). Saponins are compounds made of sugar units linked to a fat-soluble triterpene or steroid base (Chen et al. 2024). They form a diverse group of natural substances found in both land and marine organisms (Timilsena et al. 2023).

Phytochemically, saponins exhibit a broad spectrum of bioactivities, including hemolytic, anti-inflammatory, antibacterial, antifungal, antiviral, insecticidal, cytotoxic, and molluscicidal activities (Cankaya and Somuncuoglu 2021). They also have a cholesterol-lowering effect and serve as precursors for the semi-synthesis of steroid drugs (Sharma et al. 2023). Their therapeutic benefits are attributed to their interaction with biological membranes, which can lead to increased permeability or hemolysis of red blood cells, as well as their ability to modulate immune responses (Cao et al. 2024).

For *S. elaeagnifolium*, a moderate saponin content was found in the seeds and a low one in the leaves and fruits, especially after extraction with aqueous, dichloromethane, and methanolic solvents (Feki et al. 2014; Bouslamti et al. 2022a). These saponins are responsible for the molluscicidal activity of the plant, with seed extracts showing high bioactivity against Galba truncatula (LC_{50}: 0.94 mg/L) (Njeh et al. 2016). The enzyme-modulatory and cytotoxic effects observed in various pharmacological studies can, in part, be attributed to the presence of saponins. These findings support the hypothesis that *S. elaeagnifolium* utilizes saponins as chemical defenses both against herbivory and microbial competitors, with ecological implications in semi-arid and overgrazed habitats.

Steroidal alkaloids: Structural diversity and pharmacological importance

Steroid alkaloids are characterized by a steroid backbone containing at least one nitrogen atom, which is either located in the side chain or is incorporated into the polycyclic ring system (Xiang et al. 2022). This nitrogen atom can also be part of other heterocyclic backbones such as lactams, lactones, pyrrolidines, or pyrrolines (Remennikov 2022). These compounds are found in a number of plant families, such as Solanaceae, Apocynaceae, Buxaceae, and Liliaceae (Xiang et al. 2022). Due to their structural similarity to steroid hormones, corticosteroids, and anabolic steroids, steroidal alkaloids are also of great pharmacological interest (Abd-Karim et al. 2022). In particular, species from the Solanaceae family, such as *S. elaeagnifolium,* have produced highly active steroidal alkaloids such as solamargine and solasodine, which have cytotoxic, membrane-disrupting, and antiproliferative properties (Delbrouck et al. 2023). These properties not only contribute to potential anticancer activities but may also explain the plant's toxicity to livestock and native herbivores, which facilitates its unchecked proliferation in ecosystems with low grazing pressure (Qasem 2014). These compounds have biosynthetic processes and structures related to those of members of the Apocynaceae family, which are shrubs, herbs, and climbers mainly distributed across tropical and subtropical regions (Dey et al. 2017; Abd Karim et al. 2022).

Flavonoids: Structural diversity and multifaceted pharmacological activities

Flavonoids are a chemically heterogeneous group of naturally occurring phenolic compounds that have a widespread phenyl-benzo-pyrone ring structure (Ibrahim et al. 2021). They occur both in free and glycosidically bound form (O-glycosides and C-glycosides), the subtypes of which include flavones, flavonols, flavanones, isoflavones, chalcones, and anthocyanidins (Hu et al. 2025). Flavonoids, which are formed from phenylalanine and acetate derivatives via the shikimic acid pathway (Tohge et al. 2017), have been shown to have a variety of biological activities, such as antioxidant, anti-inflammatory, antimicrobial, anticancer, antidiabetic, and cardioprotective effects (Kakkar and Bais 2014). Their anticancer effects are intermediate in nature and are mediated through the induction of apoptosis, cell cycle arrest, inhibition of proteasome activity, and modulation of enzymes that degrade carcinogens (Hasibuan et al. 2024). Flavonoids also have anti-inflammatory effects and inhibit transcription factors for the expression of pro-inflammatory genes, including cytokines, chemokines, and eicosanoids. Therefore, they are useful in the prevention and treatment of inflammatory diseases such as arthritis, asthma, and cardiovascular diseases (Ysrafil et al. 2023). In addition, flavonoids have a strong antioxidant effect by scavenging free radicals, binding metal ions (e.g., Fe, Cu), and inhibiting ROS-forming enzymes such as microsomal monooxygenase, NADH oxidase, and glutathione S-transferase (Ibrahim et al. 2022b). These properties underline their ability to inhibit oxidative damage to lipids, proteins, and DNA. Studies on *S. elaeagnifolium* have found an abundant occurrence of flavonoids such as quercetin, kaempferol, naringin, luteolin, rutin, and apigenin, especially in the aerial parts and fruits of the plant (Bouslamti et al. 2022b; Mohammed et al. 2025). They have been found to exhibit a range of pharmacological activities, mainly anti-inflammatory activities through the downregulation of COX-2 and iNOS and antioxidant activities through the scavenging of Reactive Oxygen Species (ROS) and the induction of antioxidant enzymes such as superoxide dismutase (SOD) and catalase (Eleyan et al. 2024). In addition, glycosylated kaempferol and quercetin derivatives determined by UPLC-MS have been reported to be responsible for the hepatoprotective, antidiabetic, and enzyme inhibitory activity demonstrated in preclinical studies (Hawas et al. 2013; Bouslamti et al. 2022b).

Phenolic compounds and bioactive metabolites: Antioxidant and therapeutic potential

Phenolic compounds are the most abundant secondary metabolites that plants produce in response to biotic and abiotic stress in order to adapt and survive under the pressure of changing environmental conditions (Al-Khayri et al. 2023). These compounds, hydroxyl derivatives of aromatic rings, are either phenolic acids (one aromatic ring) or polyphenols (more than one aromatic ring) (Rahman et al. 2022). The hydroxyl side chains of these compounds are the reason for their specific biochemical functions (Zhang et al. 2022). Most plant phenols occur as glycosides, which are formed by the binding of phenol rings to sugar or acetylated sugar molecules (Bié et al. 2023). They can be further classified into phenolic acids, flavonoids, polyphenolic amides, and other non-flavonoid polyphenols based on the structure of their aglycones with a molecular weight of 500 to 4000 Da. Phenols are present in free and bound form. The bound forms are often not changed in the stomach and small intestine and then become bioactive in the large intestine (Sahraeian et al. 2024).

These phenolic compounds are antioxidants that scavenge free radicals (Ibrahim et al. 2022a). Their antioxidant activity depends on the position and number of hydroxyl groups and the substitution types on their aromatic rings (Platzer et al. 2022). They are metal chelating agents, reducing agents, hydrogen donors, and lipid peroxide scavengers and protect DNA from oxidative damage (Platzer et al. 2022). In this way, phenols are of crucial importance for the neutralization of reactive oxygen species and the protection of human health against oxidative stress (Kruk et al. 2022). Phytochemical analysis of *S. elaeagnifolium* revealed a broad spectrum of phenolic acids, including gallic acid, chlorogenic acid, vanillic acid, cinnamic acid, and p-coumaric acid, which are predominantly found in leaves and fruits (Bouslamti et al. 2022b; Mohammed et al. 2025).

The phenolic acids had both strong antioxidant and enzyme inhibitory activities. For example, gallic acid demonstrated antiglycation activity comparable to reference compounds in vitro, while chlorogenic and vanillic acids showed favorable molecular docking interactions with the active site of carbonic anhydrase II (Feki et al. 2014; Mohammed et al. 2025). The cumulative presence of such phenolics contributes significantly to the plant's therapeutic potential, particularly in oxidative stress-related disorders and metabolic syndrome (Sun and Shahrajabian 2023). The bioactivity of *S. elaeagnifolium* can be largely attributed to its complex secondary metabolite profile, particularly its flavonoids and steroidal alkaloids. Evidence from multiple papers (Hawas et al. 2013; Al-Hamaideh et al. 2020; Bouslamti et al. 2022a, et al. 2024; Mohammed et al. 2025), confirms the presence of key pharmacophores responsible for diverse molecular actions. Gallic acid, for example, had in vitro antiglycation activity comparable to the reference compounds, while chlorogenic and vanillic acids also had good molecular docking interaction with the active site of carbonic anhydrase II (Feki et al. 2014; Mohammed et al. 2025). Experimental results from a series of papers (Hawas et al. 2013; Al-Hamaideh et al. 2020; Bouslamti et al. 2022a, et al. 2024; Mohammed et al. 2025), confirm the presence of important pharmacophores providing various molecular activities.

The phytochemical profiling of *S. elaeagnifolium* leaf extracts revealed significant differences in total phenolic and flavonoid content depending on the extraction solvent. Ethanol extract exhibited the highest yield (6.80%) and the greatest concentration of total phenolic compounds (158.77±1.46 mg GAE/g) compared to ethyl acetate and acetone (79.04±0.98 and 41.78±0.14 mg GAE/g, respectively). However, ethyl acetate extract showed the highest total flavonoid content (134.31±0.04 mg QE/g), while acetone and ethanol extracts showed slightly lower values. Regarding enzyme inhibition, both ethanol and acetone extracts demonstrated strong α-amylase inhibitory activity with IC_{50} values of 17.78±2.38 µg/mL and 17.96±6.05 µg/mL, respectively comparable to the standard drug acarbose (15.28±0.43 µg/mL). In α-glucosidase inhibition, ethanol extracts again proved most potent (27.90±5.02 µg/mL), followed by acetone (36.44±3.30 µg/mL), while ethyl acetate showed a weaker inhibitory effect (59.76±13.66 µg/mL). These results support the potential of *S. elaeagnifolium* ethanol extracts in managing hyperglycemia through dual enzyme inhibition (Xavier et al. 2024). Furthermore, quercetin and kaempferol derivatives may contribute to allelopathic interactions, as supported by comparable studies in related Solanaceae species (Bouslamti et al. 2022a).

Flavonoid-mediated pathways

UPLC-MS and high-resolution HPLC profiling of fruit and aerial extracts showed the dominance of quercetin in addition to kaempferol, naringin, luteolin, and apigenin (Bouslamti et al. 2022a; Mohammed et al. 2025). Quercetin and kaempferol indeed control inflammation and oxidative stress through the enhancement of the cellular antioxidant system and inhibiting the release of cytochrome-c from mitochondria (Ibrahim et al. 2021). This, in turn, leads to reduced expression of apoptosis-related genes such as Bax and caspase-3, ultimately protecting against cell apoptosis and histopathological alterations (Ibrahim et al. 2020). These flavonoids counteract the activity of ROS, boost antioxidant enzymes (e.g., SOD, catalase), and suppress pro-inflammatory mediators (TNF-α, IL-6) (Eleyan et al. 2018a; Bouslamti et al. 2022b). Such cytoprotective mechanisms suggest that *S. elaeagnifolium* could serve as a phytopharmaceutical model species for developing antioxidants adapted to oxidative stress conditions characteristic of arid and semi-arid zones.

Anti-inflammatory signaling

Experimental carrageenan-induced paw edema showed that the extracts leaf extracts and fruit) had the same anti-inflammatory effect as indomethacin ($p<0.001$). The effect is via inhibition of COX-2 and iNOS due to the high content of quercetin and flavones (Bouslamti et al. 2022a). This aligns with studies showing similar anti-inflammatory effects in related invasive *Solanum* species in Mediterranean and North African habitats, reinforcing cross-regional relevance (Sayari et al. 2022).

Steroidal alkaloids and cytotoxicity

The steroidal alkaloids solamargine and solasodine, which are found in both ripe and unripe berries, show cytotoxicity against the colon cancer cell lines HT29, HCT116, SW620, and CACO2. The alkaloids were found to destabilize mitochondrial membranes, induce apoptosis, and inhibit DNA replication of cancer cells (Al-Hamaideh et al. 2020). As hypothesized in the present review, the molecular pharmacology of *S. elaeagnifolium* is probably determined by its high polyphenolic metabolites and steroidal alkaloids content. Notably, this selective cytotoxicity supports the dual ecological and therapeutic relevance of these compounds, potentially reducing herbivory while offering pharmacological leads.The secondary metabolites have been consistently found to exert functions in the control of important biological processes such as modulation of inflammatory processes, antioxidant activity, liver protection, regulation of blood glucose levels, and antiproliferation (Dey et al. 2019). Overall, these results highlight the overall therapeutic potential of the plant and suggest that further in-depth mechanistic research is needed to identify the underlying molecular targets and pathways.

Fatty acids and oils

Plant oils have been sought after for centuries for their medicinal and fragrant properties. These oils are obtained by various methods: cold pressing, solvent extraction, steam distillation, and newer microwave-assisted techniques, and they have various uses in perfumery, cosmetics, aromatherapy, phytotherapy, nutrition, and pest control (Hassid et al. 2025). In medicine, they are used for their gastroprotective, antiemetic, antibacterial, antifungal, antiviral, antioxidant, antidiabetic, antimutagenic, and anticancer effects (Ramesh and Muthuraman 2018; Pezantes-Orellana et al. 2024). Although the detailed lipidomic profiles of the seed oil of *S. elaeagnifolium* still need to be clarified, preliminary observations indicate the presence of essential fatty acids such as linoleic acid and oleic acid. These are responsible for the emollient and antimicrobial effects of the oil and justify its traditional use in the production of soap and biodiesel. Further characterization of the seed oil's constituents is required to evaluate its full therapeutic and industrial potential (Bouslamti et al. 2024). In arid areas like Gaza, such multi-use seed oils could serve as renewable bioresources for rural industry development.

Mineral composition and nutritional profile

Quantitative analysis of *S. elaeagnifolium* revealed a high mineral content, especially in the leaves, which had consistently higher concentrations of all major elements except phosphorus compared to the fruits (Bouslamti et al. 2024). Calcium (1815.45 mg/100 g) and potassium (1624.63 mg/100 g) were the predominant minerals in the leaves, with significant amounts of magnesium and phosphorus. In addition, physiologically effective amounts of trace elements such as iron, zinc, and copper were found. In contrast, the fruits contained comparatively moderate amounts of potassium and magnesium but much lower amounts of calcium and phosphorus.

Above all, the toxic heavy metals cadmium, chromium, and selenium were absent or below the detection limit, which completes the safety profile of the plant for food and nutraceutical purposes (Bouslamti et al. 2024). Taken together, these mineral findings underline not only the nutritional and pharmacological importance of *S. elaeagnifolium* but also its potential value as an additional source of minerals, particularly in settings where micronutrient deficiencies prevail. Among the compounds identified, kaempferol 8-C-β-galactoside and various kaempferol glycosides such as kaempferol 8-C-, 6-C-, 7-O-, and 3-O-glucosides represent relatively new flavonoid derivatives isolated from the aerial parts of the plant. Despite their structural uniqueness and potential biological relevance, there is a noticeable lack of experimental studies investigating their pharmacological activities. This highlights a significant research gap that warrants further exploration to fully understand their therapeutic potential.

A detailed listing of these bioactive molecules, including their type, plant part distribution, and references, is provided in Table 7 and Figure 5. A wide variety of secondary metabolites—including flavonoids, alkaloids, tannins, saponins, and steroidal compounds have been detected in different parts of *S. elaeagnifolium*. Their levels vary depending on the plant organ analyzed and the extraction method used. These findings are comprehensively summarized in Table 6, which outlines the presence levels of each compound type in the leaves, fruits, and seeds of the plant (Table 6). This nutritional richness may contribute to the resilience of *S. elaeagnifolium* in nutrient-poor soils and also explains its historical integration into traditional food-medicine systems despite its toxic potential.

Antioxidant and enzyme inhibition activities

Phenolic compounds are the most variable class of plant secondary metabolites induced by abiotic and biotic stress factors, and they are important adaptive compounds under changing environmental conditions. Natural antioxidants can participate in potential antioxidant treatments to protect cells from oxidative stress. Consequently, there is a requirement to distinguish other natural and safer sources of antioxidants. In ecosystems like the Gaza Strip, where populations rely on local flora for health support, such naturally occurring antioxidants from wild plants offer culturally acceptable and low-cost alternatives to synthetic drugs. Cumulative evidence has reported that phenolic compounds possess several biological and pharmacological activities, such as anti-inflammatory, antioxidant, and anti-apoptotic properties, through inhibition of the pro-apoptotic effects accompanied by a lowering of caspase-3 activity (Eleyan et al. 2025).

Table 6. Summary of secondary metabolites detected in different parts of *Solanum elaeagnifolium*

Compound type	Plant part	Presence level	References
Flavonoids	Leaves	+++	(Feki et al. 2014; Bouslamti et al. 2024)
Flavonoids	Fruits	++++	(Houda et al. 2014)
Flavonoids	Seeds	++	(Feki et al. 2014)
Alkaloids	Leaves, Fruits, Seeds	++	(Feki et al. 2014; Bouslamti et al. 2024)
Tannins	Leaves, Fruits, Seeds	++	(Feki et al. 2014; Bouslamti et al. 2024)
Polyphenols	Leaves	+++	(Feki et al. 2014; Bouslamti et al. 2024)
Polyphenols	Fruits	+++	(Bouslamti et al. 2022b)
Saponins	Leaves, Fruits	++	(Feki et al. 2014; Bouslamti et al. 2024)
Saponins	Seeds	+++	(Feki et al. 2014)
Steroids/Triterpenes	Leaves, Fruits	++	(Feki et al. 2014; Bouslamti et al. 2024)
Steroids/Triterpenes	Seeds	+++	(Feki et al. 2014; Bouslamti et al. 2024)
Carotenoids, Tropolones, Quinones	All parts	-	(Feki et al. 2014)

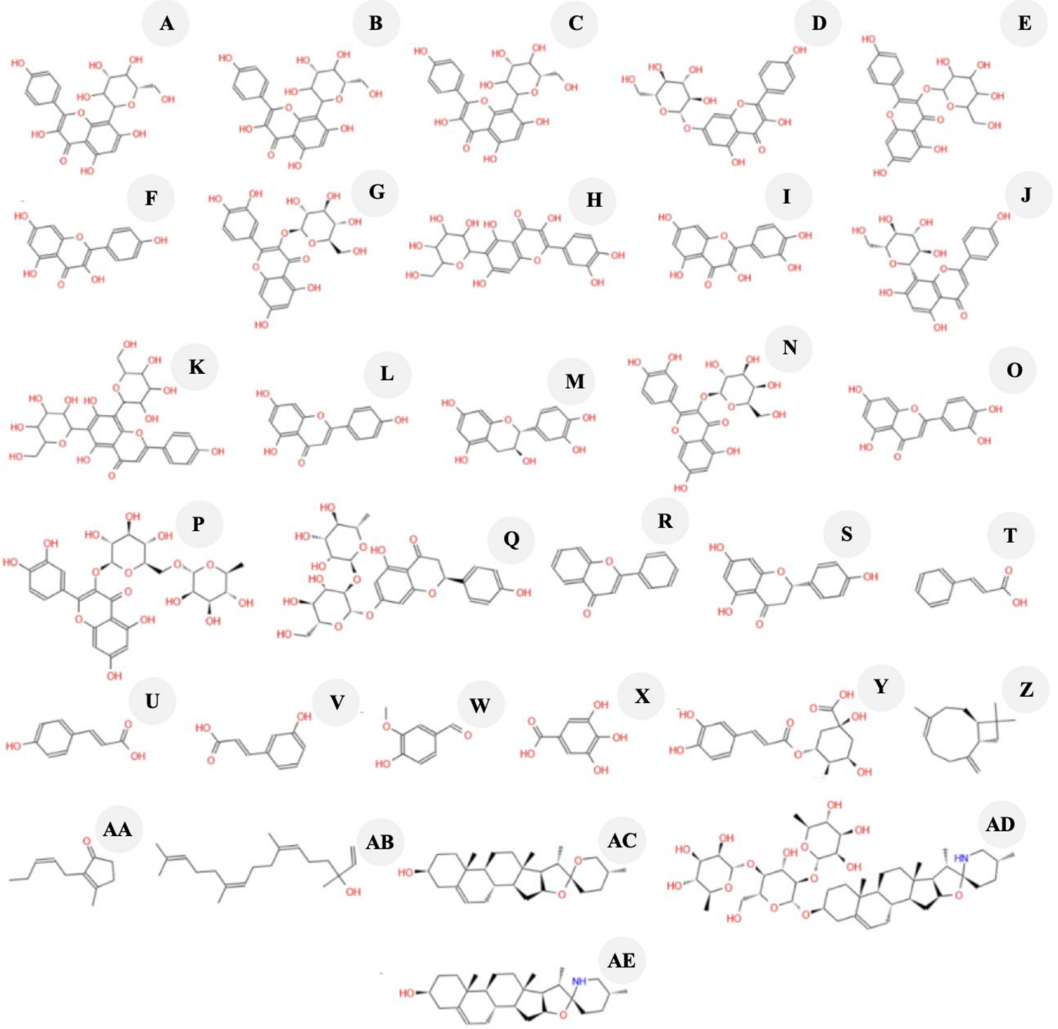

Figure 5. Chemical structures of major bioactive compounds identified in *Solanum elaeagnifolium*, these include: A. Kaempferol 8-C-β-galactoside; B. Kaempferol 8-C-glucosides; C. Kaempferol 6-C-glucosides; D. Kaempferol 7-O-glucosides; E. Kaempferol 3-O-glucosides; F. Kaempferol; G. Quercetin 3-O-glycosides; H. Quercetin 6-C-glycosides; I. Quercetin; J. Vitexin; K. Vicenin II; L. Apigenin; M. Catechin; N. Hyperoside; O. Luteolin; P. Rutin; Q. Naringin; R. Flavone; S. Naringenin; T. Cinnamic acid; U. p-coumaric acid; V. Trans-3-hydroxycinnamic acid; W. Vanillin; X. Gallic acid; Y. Chlorogenic acid; Z. (E)-Caryophyllene; AA. (Z)-Jasmone; AB. Geranyl linalool isomer; AC. Diosgenin; AD. Solamargine; AE. Solasodine

Table 7. Major bioactive compounds in different parts of *Solanum elaeagnifolium*

Compound name	Chemical class	Plant part	Bioactivity	Assay type	Mechanistic insight	Extraction method	References
Kaempferol 8-C-β-galactoside Kaempferol 8-C-/6-C-/7-O-/3-O-glucosides	Flavonoid glycosides	Aerial parts	Antioxidant, Antiglycating	In Vitro	Scavenges free radicals	Aqueous methanolic extract (chromatography)	(Hawas et al. 2013; Ahmad et al. 2016; Kluska et al. 2022)
Kaempferol	Flavonol	Leaf, Fruit, Aerial parts	Anti-inflammatory, antioxidant	In Vitro	Inhibits COX pathways	Ethanolic extract (HPLC)	(Sharma et al. 2021; Bouslamti et al. 2023; Mohammed et al. 2025)
Quercetin 3-O-/6-C-glycosides	Flavonoids	Aerial parts	Antioxidant	In Vitro	Scavenges ROS	Methanolic extract (HPLC)	(Hawas et al. 2013; Jan et al. 2022; Bouslamti et al. 2023)
Quercetin	Flavonol	Leaf and Fruit	Antioxidant, anti-inflammatory, antiapoptotic	In Vitro, In Vivo	Inhibits NF-κB, activates intrinsic (mitochondrial) pathway	Hydro-ethanolic extract (HPLC)	(Bouslamti et al. 2022b, et al. 2023; Eleyan et al. 2024)
Vitexin	C-glycosides	Aerial parts	Antioxidant, anti-inflammatory, anticancer	In Vitro, In Vivo	Reduces oxidative stress and inhibits NO, TNF-α, and MAPK activation.	Aqueous methanolic extract (chromatography)	(Hawas et al. 2013; Babaei et al. 2020)
Vicenin II	C-glycosides	Aerial parts	Antioxidant, Anti-inflammatory	In Vitro	Upregulates antioxidant enzymes and blocks NF-κB translocation	Aqueous methanolic extract (chromatography)	(Hawas et al. 2013; Duan et al. 2019)
Apigenin	Flavone	Root, Aerial parts	Anti-inflammatory, anticancer, Antidiabetic	In Vitro, In Vivo	Induces apoptosis, inhibits NF-κB and α-glucosidase, and enhances insulin secretion.	Methanolic extract (HPLC)	(Salehi et al. 2019; Al-Hamaideh et al. 2020; Al-Hamaideh 2023)
Catechin	Flavan-3-ol	Fruit	Antioxidant, antibacterials	In Vitro, In Vivo	Prevents lipid peroxidation, enhances cytoprotective enzymes, and disrupts bacterial membranes.	Ethanolic extract (HPLC)	(Wu and Brown 2021; Bouslamti et al. 2023; Yuhan et al. 2023)
Hyperoside	Flavonoid	Root, Flowers	Antioxidant, anti-inflammatory, and anti-tumor	In Vitro, In Vivo	Activates Nrf2/HO-1, Wnt/β-catenin, and Hedgehog pathways; induces apoptosis.	Methanolic extract (HPLC)	(Al-Hamaideh et al. 2020; Zhang et al. 2025)
Luteolin	Flavone	Aerial parts, Leaf and Fruit	Anti-inflammatory, Antioxidant, Anticancer	In Vitro, In Vivo	Blocks pro-inflammatory cytokines, upregulates antioxidant genes, and inhibits mTOR, STAT3, and Wnt/β-catenin pathways.	Hydro-ethanolic extract (HPLC)	(Bouslamti et al. 2022b; Al-Hamaideh 2023; Almatroodi et al. 2024)
Rutin	Flavonoid glycoside	Leaf and Fruit	Vasoprotective, antioxidant, anti-diabetic	In Vitro, In Vivo	Suppresses proinflammatory cytokines and induces p53 and antioxidant enzymes.	Methanolic extract (HPLC)	(Ganeshpurkar and Saluja 2017; Bouslamti et al. 2023)
Naringin	Flavonoid glycoside	Leaf, Root	antioxidant, anti-inflammatory, and anti-cancer	In Vitro, In Vivo	Scavenges free radicals, inhibits proliferation, and induces apoptosis and cell cycle arrest.	Methanolic extract (HPLC-DAD)	(Al-Hamaideh 2023; Bouslamti et al. 2023; He and Zhang 2023)
Flavone	Flavone	Leaf	Antioxidant and Anti-inflammatory	In Vitro, In Vivo	Inhibits XO, COX, and PI3K; enhances antioxidant enzymes; scavenges radicals. 2/2	Aqueous extract (HPLC-DAD)	(Panche et al. 2016; Bouslamti et al. 2023)

Naringenin	Flavonone	Leaf and Fruit	Anti-inflammatory, antioxidant, anti-diabetic, anti-atherosclerotic, and anti-cancer	In Vitro	Scavenges free radicals, improves insulin sensitivity, reduces lipids, and induces apoptosis.	Hydro-ethanolic extract (HPLC)	(Alam et al. 2014; Bouslamti et al. 2022b)
Cinnamic acid	Phenolic acid	Leaf	Antioxidant, Anti-inflammatory, Antimicrobial, antifungal	In Vitro	Inhibits lipid peroxidation, disrupts membranes, blocks mTOR/PI3K/AKT, and induces apoptosis.	Ethanolic extract (HPLC)	(Ruwizhi and Aderibigbe 2020; Bouslamti et al. 2023; Peng et al. 2024)
p-coumaric acid	Phenolic acid	Leaf	Antioxidant, Antimicrobial, Anti-proliferative	In Vitro	Scavenges ROS, damages bacterial DNA and membranes, and induces apoptosis via mitochondrial disruption.	Ethanolic extract (HPLC)	(Bouslamti et al. 2023; Zaman et al. 2023)
Trans-3-hydroxycinnamic acid	Phenolic acid	Leaf	Antioxidant	In Vitro	Neutralizes free radicals	Ethanolic extract (HPLC)	(Bouslamti et al. 2023; Khawula et al. 2023)
Vanillin	Phenolic aldehyde	Fruit	Antioxidant, Neurodegenerative, Anti-Inflammatory, Antibacterial, Anti-Cancer	In Vitro, In Vivo	Reduces oxidative stress, inhibits NF-κB, COX-2, MAPK, and HIF-1α pathways, and suppresses mTOR and ERK signaling.	Ethanolic extract (GC-MS)	(Bouslamti et al. 2023; Iannuzzi et al. 2023; Kafali et al. 2024)
Gallic acid	Phenolic acid	Leaf and Fruit	Antioxidant, Antimicrobial, Anti-inflammatory, Anticancer	In Vitro, In Vivo	Reduces mitochondrial ROS and inflammation, inhibits biofilm formation, and regulates cell cycle proteins.	Methanolic extract (HPLC)	(Bouslamti et al. 2022b)
Chlorogenic acid	Phenolic acid	Flowers, Aerial parts	Hepatoprotective, antioxidant	In Vivo	Prevents liver injury via ROS control	Methanolic extract (UPLC-MS)	(Kahkeshani et al. 2019; Al-Hamaideh 2023)
(E)-Caryophyllene	Sesquiterpene	Leaf	Anti-inflammatory, obesity, non-alcoholic fatty liver disease/nonalcoholic steatohepatitis (NAFLD/NASH) liver diseases, diabetes, cardiovascular diseases, pain and other nervous system disorders	In Vitro	Reduces inflammation via cytokine suppression, CB2 receptor activation, and PPAR interaction.	Essential oil (GC-MS)	(Tsaballa et al. 2015; Scandiffio et al. 2020)
(Z)-Jasmone	Jasmonate-derived volatile	Leaf	antimicrobial Wound healing	In Vitro, In Vivo	Dual damage mechanisms, Promotes cell migration and repair	Volatile oil (GC-MS)	(Tsaballa et al. 2015; Venkadakrishnan et al. 2024)
Geranyl linalool isomer	Diterpene alcohol	Leaf	anti-inflammatory, antioxidant, Neuroprotective	In Vitro, In Vivo	Enhances cytoprotective enzymes, reduces lipid peroxidation, and prevents neural cell death.	Essential oil (GC-MS)	(Tsaballa et al. 2015; Pereira et al. 2018)
Diosgenin	Steroidal sapogenin	Root, Flowers, Aerial parts	Neuroprotective, Anticancer	In Vitro, In Vivo	Suppresses neuronal apoptosis, enhances survival pathways, and induces cell cycle arrest via p38α-MAPK.	Ethanolic extract (HPLC)	(Semwal et al. 2022; Al-Hamaideh 2023)
Solamargine	Steroidal alkaloid	Root, Flowers, Aerial parts	Anticancer, cytotoxic	In Vitro	Induces cancer cell apoptosis	Ethanolic extract (HPLC)	(Kalalinia and Karimi-Sani 2017; Al-Hamaideh 2023)
Solasodin	Steroidal alkaloid	Root, Flowers, Aerial parts	Antioxidant, Neuroprotective, Anti-inflammatory, Anticancer	In Vitro, In Vivo	Reduces lipid peroxides and NO, boosts antioxidant enzymes, and inhibits AKT/GSK-3β/β-catenin pathway.	Ethanolic extract (HPLC)	(Zhuang et al. 2017; Al-Hamaideh 2023)

Phenolic compounds are powerful antioxidants, primarily because of their free radical scavenging activity. The degree and position of the hydroxyl groups and the type of substituents on their aromatic rings determine their antioxidant activity. They act as reducing agents, hydrogen atom donors, metal ion chelators, inhibitors of lipid peroxidation, and protective agents against oxidative DNA damage. These diverse actions of phenolic compounds position them as key modulators in redox homeostasis and cellular protection (Chaachouay and Zidane 2024). Of the extracts tested, the methanolic seed and fruit extracts showed the strongest antioxidant activities based on DPPH radical scavenging assays. The fruit extract (SEFR) showed a DPPH IC_{50} of 0.035±0.006 mg/mL and a FRAP EC_{50} of 83.46±7.69 µg/mL (Bouslamti et al. 2022b). In addition, the Total Antioxidant Capacity (TAC) was 939.66 µg AAE/mg, indicating strong free radical scavenging activity. Further studies have shown that different parts of *S. elaeagnifolium* have different enzyme inhibitory activities than those described in leaf and fruit extracts.

Pharmacological studies showed that flower and root extracts exhibited strong inhibition of Pancreatic Lipase (PL) with IC_{50} values of 34.9 µg/mL and 38.25 µg/mL, respectively, while extracts from the aerial parts showed no significant inhibition (Bouslamti et al. 2024). This organ-specific activity suggests that bioactive compound distribution varies within the plant and reflects adaptive strategies for different ecological pressures across tissues. In addition, the roots and flowers suppressed starch hydrolysis with IC_{50} values of 2.7 and 3.01 mg/mL and reduced sugar release at 100 mg/mL to 2.47 and 2.25 mmol, respectively. The enzyme inhibition profiles, and associated starch digestion effects of different plant parts are summarized in Table 9.

The results show a semi-specific inhibition of enzymatic activity and enhance the antidiabetic effect of *S. elaeagnifolium*. This semi-selective inhibition pattern may reflect the structural affinity of individual phytochemicals to specific digestive enzymes, which could be leveraged in selective nutraceutical designs for diabetes and obesity. The antioxidant and enzyme inhibitory activities of the plant are largely attributed to its high content of phenolic and flavonoid compounds, which are highly concentrated in the fruit and seed extracts. Evidence from multiple studies, (Al-Hamaideh et al. 2020; Bouslamti et al. 2022b, et al. 2024; Mohammed et al. 2025), consistently supports the bioactivity and therapeutic promise of this species. The antioxidant potential of *S. elaeagnifolium* leaf extracts varied by solvent. Ethanol extract showed the strongest overall activity, including superoxide radical scavenging, FRAP, and metal chelation. Acetone extract exhibited the highest DPPH and PHM activities, while ethyl acetate was the weakest. Ascorbic acid performed best as the reference. Ethanol was the most effective solvent for extracting antioxidant compounds (Xavier et al. 2024). A comparative summary of the antioxidant assays and enzyme inhibition results from various plant parts is presented in Table 8. Such activity highlights the plant's potential in managing oxidative stress-associated disorders including aging, cardiovascular diseases, and diabetes (Ibrahim et al. 2022b). These properties, along with its traditional usage and availability in arid ecosystems, position *S. elaeagnifolium* as a promising phytopharmacological candidate for integrative medicine, especially in under-resourced regions.

Multivariate analysis of phytochemical and antioxidant profiles

In order to visualize the patterns and clustering of the extracts according to phytochemical and antioxidant profile, a hierarchical heat map with standardized values was created. As shown in Figure 6, the samples were clustered according to similarity of their total phenols (TPC), flavonoids (TFC), DPPH IC_{50}, ABTS IC_{50} and ferric reducing power (FRP). The heat map showed clear cluster patterns by plant part and solvent. Both seed extracts (seed ethanol and seed acetone) were clustered with high TPC and moderate antioxidant activity. Fruit extracts were separated in a cluster with relatively low FRP and higher flavonoid content. Leaf extracts, especially with acetone, showed strong clustering due to higher antioxidant activity and TFC. These results show that both the plant part and the solvent have an influence on the biochemical profile and bioactivity of the extracts. The heat map allows a more accurate discrimination than PCA and promotes the grouping of extracts based on their bioactive compounds.

Enzyme inhibition (anti-obesity and antidiabetic effects)

Pancreatic Lipase (PL) inhibition assays showed a dose-dependent response, with fruit extracts showing a stronger inhibitory effect (IC_{50}: 0.106±0.0008 mg/mL) than the standard drug orlistat (IC_{50}: 0.128±0.003 mg/mL) (Bouslamti et al. 2022b). The fruit extract also showed remarkable efficacy (IC_{50}: 0.167±0.0006 mg/mL), indicating the plant's potential role in reducing fat absorption and treating obesity.

In carbohydrate digestion assays, both leaf and fruit extracts effectively inhibited α-amylase and α-glucosidase, enzymes responsible for the breakdown of starch and sugar, resulting in a decrease in postprandial blood glucose levels in vivo (Xavier et al. 2024). Their inhibitory effects were comparable to those of acarbose, with fruit extracts performing better in oral glucose tolerance tests (Bouslamti et al. 2022b). Like acarbose, the extracts inhibit α-glucosidase and α-amylase, lowering postprandial glucose in oral glucose tolerance tests. Mechanisms include disruption of carbohydrate digestion and enhanced glucose uptake (Bouslamti et al. 2022b). The potent inhibition of pancreatic lipase by *S. elaeagnifolium* suggests a survival advantage in arid and semi-arid environments where competition for water and nutrients is high (Amalraj et al. 2021). By deterring herbivory through lipase-inhibiting compounds, the plant limits predation and enhances its invasive capacity. These dual ecological and pharmacological traits warrant further mechanistic studies in invasive species biology. These findings align with studies from Mediterranean and African arid ecosystems, where other *Solanum* species exhibit similar antidiabetic and anti-obesity activities (e.g., *S. incanum*, *S. nigrum*) (Andargie et al. 2022). Such functional convergence supports the hypothesis that plants adapted to xeric environments often evolve bioactive compounds that serve both ecological defense and therapeutic functions.

Docking studies and molecular evidence

In silico docking revealed that phenolic acids (e.g., 4-hydroxybenzoic acid and vanillic acid) are tightly bound to the active site of carbonic anhydrase II. The results confirm the biochemical activity observed in vitro and reveal structure-activity relationships that are relevant for the inhibition of the enzyme (Mohammed et al. 2025). The present review highlights the strong antioxidant and enzyme inhibitory properties of *S. elaeagnifolium*, mainly due to its diverse phytochemical composition, especially its flavonoid and phenolic acid constituents' quercetin, rutin, kaempferol, and gallic acid.

The bioactive constituents are responsible for protecting against oxidative stress and the plant's important properties in regulating metabolic enzymes associated with diabetes and metabolic disorders. Taken together, the evidence supports the therapeutic prospects for *S. elaeagnifolium* as a potential natural agent for the therapy of oxidative and metabolic syndromes that is worthy of pharmacological and clinical investigation. The ability of phenolic acids to bind key metabolic enzymes not only explains their antidiabetic potential but may also relate to allelopathic interactions with competing flora (Mushtaq and Fauconnier 2024). By interfering with carbohydrate metabolism in surrounding plants, these compounds might contribute to the competitive dominance of *S. elaeagnifolium* in resource-limited habitats (Latif et al. 2017) such as the Gaza Strip.

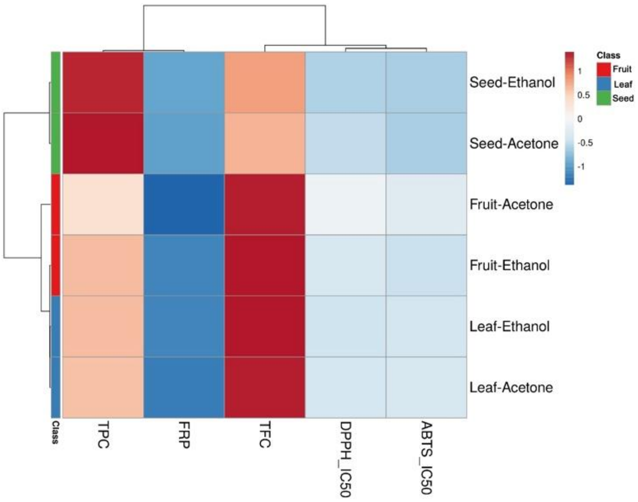

Figure 6. Heatmap showing standardized values of total phenolics (TPC), flavonoids (TFC), and antioxidant activities (DPPH IC$_{50}$, ABTS IC$_{50}$, FRP) across six plant extracts. Rows (samples) and columns (variables) were clustered using correlation distance and average linkage. Distinct patterns were observed among leaf, fruit, and seed extracts, reflecting differences in bioactive compound composition and antioxidant potential

Table 8. Antioxidant and enzyme inhibition activities of *Solanum elaeagnifolium*

Plant part	Assay	Result	References
Seed	DPPH IC$_{50}$	0.025 mg/mL (Acetone), 0.042 mg/mL (Methanol), 0.029 mg/mL (Aqueous)	(Feki et al. 2014)
Fruit (Overripe)	DPPH	7203 µmol TE/g (Methanol)	(Houda et al. 2014)
Fruit	ORAC, ABTS IC$_{50}$	4087 µmol TE/g (Methanol, ORAC), 2.5 µg/mL (Aqueous, ABTS)	(Houda et al. 2014)
Leaf	DPPH IC$_{50}$, FRAP EC$_{50}$, TAC	132.46±11.73 µg/mL (Hydroethanolic, DPPH), 462.36±10.43 µg/mL (FRAP), 890.10±7.76 µg AAE/mg (TAC)	(Bouslamti et al. 2022b)
Fruit	DPPH IC$_{50}$, FRAP EC$_{50}$, TAC	35.15±6.09 µg/mL (Hydroethanolic, DPPH), 83.46±7.69 µg/mL (FRAP), 939.66±5.01 µg AAE/mg (TAC)	(Bouslamti et al. 2022b)
SEFE	Lipase IC50/Antiglycation IC50	0.167 mg/mL/3.99 mg/mL	(Feki et al. 2014)
SEFR	Lipase IC50/Antiglycation IC50	0.106 mg/mL/3.997 mg/mL	(Feki et al. 2014)
Orlistat	Lipase IC50	0.128 mg/mL	(Bouslamti et al. 2024)
Gallic Acid	Antiglycation IC50	3.008 mg/mL	(Feki et al. 2014)

Table 9. Enzyme inhibition and starch digestion activity of different plant parts of *Solanum elaeagnifolium* (Bouslamti et al. 2024)

Plant part	PL IC50 (µg/mL)	Starch digestion IC50 (mg/mL)	Sugar interference at 100 mg/ml (mmol)
Flowers	34.9	2.7	2.47
Roots	38.25	3.01	2.25
Aerial parts	Non-inhibitory	Non-inhibitory	-

Anti-cancer and anti-glycation activity

Several bioactive molecules isolated from *S. elaeagnifolium* have been associated with anticancer and antiglycemic activity. However, their biological effects appear to be highly dependent on the part of the plant used, the extraction method used, and the dose administered (Feki et al. 2014; Al-Hamaideh et al. 2020). These findings advocate for further fractionation and bioassay-guided isolation to identify active principles (Ibrahim et al. 2022b). However, the observed IC_{50} values remain above the NCI efficacy threshold of 30 µg/mL, indicating limited standalone potency (Canga et al. 2022). These extracts may still be valuable as adjuvants or scaffolds for semi-synthetic derivatization pending bioavailability and pharmacokinetics optimization.

Antiproliferative activity

In vitro studies have shown that the extract from the plant parts and the hydroethanolic extract of the flowering plant selectively inhibited the growth of colon cancer cell lines CACO2, SW480, HT29, and HCT116. The extract from the plant part provided an IC_{50} value of 121.5±18.2 µg/mL against HCT116 cells, while the flower extract provided an IC_{50} value of 66.3±5.5 µg/mL against CACO2 cells. These cytotoxicity results across different cancer cell lines are summarized in Table 10, which compares the anti-proliferative activity of various plant parts of *S. elaeagnifolium*. Despite these results, none of the extracts tested achieved the IC_{50} value of less than 30 µg/mL required by the National Cancer Institute to classify the compounds as good anticancer candidates (Feki et al. 2014).

Relevant secondary metabolites

These active compounds, such as solamargine, solasodine, and diosgenin, in the aerial parts, flowers, and roots have previously been linked to mechanisms such as apoptosis and DNA fragmentation in cancer cells (Feki et al. 2014). In addition, the flavonoid molecules quercetin, kaempferol, and flavone glycosides have pro-apoptotic and antioxidant effects and tend to modulate oxidative stress in cancer cells (Al-Hamaideh et al. 2020; Ibrahim et al. 2021). These cytotoxic effects may reflect a natural ecological adaptation, as many invasive species evolve phytochemicals to deter herbivores or suppress neighboring plants (Ain et al. 2023). The presence of apoptosis-inducing steroidal alkaloids in *S. elaeagnifolium* may thus serve dual ecological and therapeutic functions. Comparable antiproliferative effects have been reported in xerophytic *Solanum* species from Mediterranean and North African ecosystems, underscoring the relevance of dryland-adapted plants as sources of cytotoxic agents (Gafforov et al. 2024). It is particularly noteworthy that a study in the Negev desert found that aqueous extracts from the aerial parts of *S. elaeagnifolium* were over 97% cytotoxic to melanoma cell lines (Feki et al. 2014). This strong deviation from other research results can possibly be explained by the different content of phytochemicals in the different regions or the different extraction methods.

Antiglycation activity

S. elaeagnifolium exhibits significant antiglycation properties. Both the leaf and fruit extracts demonstrated strong inhibitory effects against the formation of Advanced Glycation End products (AGEs) in a hemoglobin glycation assay. The IC_{50} values were 3.997±0.140 mg/mL for leaf extract and 3.990±0.236 mg/mL for fruit extract, closely comparable to the reference standard gallic acid, which exhibited an IC_{50} of 3.008±0.03 mg/mL. These findings underscore the potential of *S. elaeagnifolium* as a promising natural antiglycation agent, which could contribute to the management of diabetic complications such as retinopathy, neuropathy, and nephropathy (Bouslamti et al. 2023).

Inhibition of hemoglobin glycation

In addition to its general antiglycation potential, *S. elaeagnifolium* demonstrated strong inhibition of hemoglobin glycation, with IC_{50} values of 3.990±0.236 mg/mL (fruit extract) and 3.997±0.140 mg/mL (leaf extract). These values are nearly equivalent to that of gallic acid, a well-established antiglycation agent (IC_{50}: 3.008±0.03 mg/mL). Despite moderate cytotoxic activity against colorectal cancer cell lines below the NCI threshold for significant activity the extracts' potent antiglycation effect supports their potential role in the prevention of glycation-mediated tissue damage in diabetes. Further in vivo validation and mechanistic elucidation are warranted to explore their therapeutic applicability (Bouslamti et al. 2023). This activity is particularly relevant in arid and resource-limited regions such as the Gaza Strip, where access to synthetic antidiabetic agents is limited. Traditional use of plants like *S. elaeagnifolium* may thus offer culturally embedded alternatives for managing chronic complications of diabetes, especially when supported by modern pharmacological validation.

Antimicrobial activity

Studies with *S. elaeagnifolium* showed that its extracts have selective antimicrobial activity against various gram-positive and gram-negative bacteria as well as fungal species. Hydroethanolic and hydroacetonic leaf and fruit extracts showed clear zones of inhibition against *Staphylococcus aureus*, *S. aureus* ATCC 6633, *Bacillus subtilis*, *B. subtilis* DSM 6333, *Escherichia coli*, *E. coli* K12, *Proteus mirabilis*, and *P. mirabilis* ATCC 29906 (Bouslamti et al. 2023; Mohammed et al. 2025). The highest antibacterial activity was observed against *E. coli* with an inhibition value of 12.33±0.57 mm and a Minimum Inhibitory Concentration (MIC) of 1.25 mg/mL.

The antibacterial activity of *S. elaeagnifolium* leaf extracts varied depending on the solvent and target bacterial strain. Ethanol extract demonstrated the strongest broad-spectrum inhibition with Minimum Inhibitory Concentration (MIC) values of 118.75 µg/mL against *E. coli*, *Proteus vulgaris*, *Staphylococcus epidermidis*, *B. subtilis*, *Rhodococcus equi*, *Salmonella typhi*, and *Shigella flexneri*. It also showed relatively potent activity against *Enterobacter aerogenes* and *Vibrio cholerae* (59.375 µg/mL), and moderate activity against *Pseudomonas aeruginosa* (29.6875 µg/mL).

In contrast, ethyl acetate and acetone extracts exhibited weaker antibacterial activity, with MIC values exceeding 950 µg/mL for several strains including *P. aeruginosa* and *E. aerogenes*. Ampicillin, used as a positive control, showed consistent and potent inhibition across all tested strains with MIC values ranging from 1.875 to 7.5 µg/mL. These findings indicate that ethanol is the most effective solvent for extracting antibacterial compounds from *S. elaeagnifolium* leaves. While the plant extracts, particularly those prepared with ethanol, demonstrated notable antibacterial effects, their potency was moderate compared to this standard (Xavier et al. 2024).

In addition, the fruit extracts inhibited *Candida albicans* and *C. albicans* ATCC 10231 with an inhibition zone of 9.00±0.50 mm and a MIC of 0.31 mg/mL. In comparison, hydroacetonic leaf extracts had little or no inhibitory effect on *C. albicans* ATCC 10231, with susceptibility varying depending on the fungal strain (Mohammed et al. 2025). The antimicrobial effect is mainly due to the plant's bioactive content of steroidal alkaloids, flavonoids, and phenolic acids (gallic acid and chlorogenic acid), which inhibit microbial cell membranes and hinder critical enzymatic activities. The inhibitory effects of different extracts against bacterial and fungal strains, including inhibition zones and MIC values, are summarized in Table 11.

Genomic and transcriptomic insights

Although genomic research on *S. elaeagnifolium* is limited, closely related *Solanum* species have demonstrated upregulation of stress-responsive genes (e.g., heat-shock proteins, antioxidant enzymes) under arid stress. RNA-seq of treated cancer cell lines exposed to seed and root extracts showed differentially expressed genes associated with apoptosis and cell cycle arrest (Al-Hamaideh et al. 2020).

A recent transcriptomics study provided deep molecular insights into the injury response of *S. elaeagnifolium*, an ecologically naturalized and invasive plant. Using a de novo transcriptome study, the researchers aimed to investigate the changes in gene expression caused by mechanical wounding, focusing on terpenoid biosynthesis, a category of specialized secondary metabolites whose importance in plant defense is well documented. Tsaballa et al. (2015) conducted next-generation sequencing of the *S. elaeagnifolium* flower and leaf transcriptome, which was successfully de novo assembled into 75,618 unigenes. Among these, numerous sequences were annotated as terpene synthases (TPSs) and key enzymes involved in both the mevalonate (MVA) and methylerythritol phosphate (MEP) pathways, which are critical for terpenoid biosynthesis (Webb et al. 2014). In addition, transcriptomic analysis of wounded leaves revealed a significant upregulation of genes such as putative 1-deoxy-D-xylulose 5-phosphate synthase 2 (DXS2) (Di and Rodriguez-Concepcion 2023). This molecular response was accompanied by a marked increase in the levels of two major terpenoids, (E)-caryophyllene and geranyl-linalool, highlighting the plant's dynamic defense response to physical injury (Falara et al. 2014).

The plant responded to mechanical wounding with a strong upregulation of genes involved in jasmonic acid signaling and of key transcription factors such as MYC2 and WRKY, which are known to play a central role in regulating plant defense responses (Luo et al. 2023; Zeng et al. 2025). The increased expression of a number of terpene synthase genes also supports the hypothesis that terpenoid biosynthesis is dynamically induced as a defense response to wounding (Zhao et al. 2021).

Table 10. Anti-proliferative activity of *Solanum elaeagnifolium*

Plant part	HT29	HCT116	SW620	CACO2	SW480	Fibroblasts	References
Flowers	3790.8	158.6	140.9	66.3	NI	3783.2	(Hawas et al. 2013; Feki et al. 2014; Al-Hamaideh et al. 2020)
Roots	NI	NI	NI	NI	NI	NI	(Hawas et al. 2013)
Aerial parts	NI	121.5	NI	132.8	696.1	103	(Feki et al. 2014; Al-Hamaideh et al. 2020)

Table 11. Antimicrobial and antifungal activities of different extracts of *S. elaeagnifolium* (Bouslamti et al. 2022a, b)

Pathogen	Extract	Inhibition zone diameter (mm)	MIC (mg/mL)
Gram-positive bacteria			
S. aureus	Fruit extract	8.66±0.57	2.5±0.00
S. aureus ATCC 6633	Hydro-ethanolic and hydro-acetonic leaf extract	-	7.5, 3.75
B. subtilis	Fruit extract	10.67±0.57	2.5±0.00
B. subtilis DSM 6333	Hydro-ethanolic and hydro-acetonic leaf extract	10.5±0.50	15, 7.5
Gram-negative bacteria			
E. coli	Leaf extract	12.33±0.57	1.25±0.00
E. coli K12	Hydro-ethanolic and hydro-acetonic leaf extract	-	7.5, 3.75
P. mirabilis	Leaf extract	11.33±0.57	-
P. mirabilis ATCC 29906	Hydro-ethanolic and hydro-acetonic leaf extract	8.25±0.75	15, 7.5
Fungal Activity			
C. albicans	Fruit extract	9.00±0.50	0.31±0.00
C. albicans ATCC 10231	Hydro-ethanolic and hydro-acetonic leaf extract	No activity reported	-

The functionally annotated transcriptomic data also revealed the presence of critical enzymatic genes of the MEP (2-C-methyl-D-erythritol 4-phosphate) and MVA (mevalonate) signaling pathways involved in terpenoid scaffold biosynthesis (Rodríguez-Concepción and Boronat 2002). Enzymes such as 1-deoxy-D-xylulose-5-phosphate synthase (DXS) and geranylgeranyl diphosphate synthase (GGPPS) were strongly represented, suggesting an induced synthesis of monoterpenes, sesquiterpenes and diterpenes in response to wound stress (Schmidt et al. 2010; Zhang et al. 2020). The study concludes that *S. elaeagnifolium's* molecular agility its capacity to quickly trigger defensive signaling pathways and produce a wide variety of bioactive terpenes plays a major role in both its ecological dominance and invasive success. Because the pathways stimulated can synthesis molecules of medicinal or economic importance, the study also offers potential phytochemical promise. These preliminary findings suggest a promising yet underexplored area of research. Therefore, more comprehensive genomic and transcriptomic investigations are strongly encouraged to uncover the molecular mechanisms underlying the plant's biological activities and adaptive responses.

GENETIC AND MORPHOLOGICAL DIVERSITY

Recent studies have shown that *S. elaeagnifolium* exhibits excellent morphological diversity in geographically isolated populations. Different growth habits, leaf morphologies and flowering patterns have been described, suggesting that the species has high intrinsic genetic diversity (Petanidou et al. 2018; Qasem et al. 2019; Singleton et al. 2020). In addition, molecular research has demonstrated extensive genetic variation even between individual populations and geographical regions (Petanidou et al. 2018; Singleton et al. 2020). The genetic heterogeneity of the plant not only reflects its ability to adapt to different environmental factors, but also makes it difficult to control and contain its proliferation.

To date, most control measures against *S. elaeagnifolium* have focused on biological control methods, particularly the use of natural enemies in the form of phytophagous insects (Lefoe et al. 2020). However, the effectiveness of such methods can be unpredictable due to the high genetic plasticity of the plant, which can determine susceptibility to biological control agents. Therefore, comprehensive management measures are now increasingly recommended for effective control, including mechanical, chemical, and biological measures in combination with preventive measures to limit seed dispersal.

MANAGEMENT STRATEGIES, CHALLENGES, AND INTEGRATED CONTROL APPROACHES FOR *S. elaeagnifolium*

The management of *S. elaeagnifolium* remains a problem due to its extremely deep, extensive root system, its long-lived seed bank, and its high regeneration capacity. Integrated control methods are considered most efficient, as single-method treatments are likely to result in regrowth or reinvasion (Uludag et al. 2016; Roberts and Florentine 2022). Mechanical suppression by repeated ploughing or mowing can temporarily contain the biomass but does not kill root fragments and dormant buds and therefore leads to rapid regrowth. Excessive tillage can even encourage the spread by breaking up rhizomes. It has been shown that even 0.5 cm long root pieces can regenerate, demonstrating the difficulty of eradication using purely mechanical methods (Tataridas et al. 2022b). Mechanical control is therefore generally only recommended when combined with the use of chemical agents against both above-ground and below-ground infestations. Chemical control through the use of systemic herbicides, particularly glyphosate and sulfosulfuron, has been found partially effective when sprayed at flowering or post-flowering stage (Tataridas et al. 2021). Nevertheless, even these herbicides are only translocated to the root system to a small extent, which reduces their overall effectiveness. In Greece, Gitsopoulos et al. (2017) reported that glyphosate (isopropylamine salt) at a dosage of 3600 g a.e. ha^{-1} provided up to 90% control when applied at the early flowering stage, but repeated treatments were required for long-term suppression (Table 12). In addition, the herbicide rimsulfuron offered promising possibilities when applied together with mechanical control or sequentially (Tataridas et al. 2022a). Preventive measures are still essential to avoid further infestation. These include early monitoring, disinfection of agricultural equipment, minimization of soil disturbance in infested fields and control of animals to reduce adventitious seed dispersal. Promoting a competitive vegetation cover of perennial grasses or legumes also prevents establishment as it masks bare soil and limits the invader's access to light and nutrients (Uludag et al. 2016). Biological pest control is a poorly researched but potentially important aspect of future management. There are no officially authorized biological control agents, but initial research has investigated the effects of herbivorous insects and fungal pathogens on this species (Tataridas et al. 2022b). Future research is needed to explore safe and ecologically sound options in this area. Due to the adaptability of the weed and its longevity in the environment, long-term control requires a multi-year, site-specific strategy that combines cultural, mechanical, and chemical control measures with public support and cross-sector collaboration. In addition to field-level control, it is important to develop policies that balance invasive species regulation with the plant's medicinal potential. This includes setting clear guidelines for safe harvesting, processing, and dosage limits, especially in communities exploring traditional remedies. Controlled bioprospecting programs could help turn *S. elaeagnifolium* into a managed resource, supporting both conservation goals and local healthcare initiatives. Such integrated approaches are especially valuable in regions like Gaza, where ecological pressures and public health needs intersect.

Table 12. Summary of herbicide efficacy on *Solanum elaeagnifolium*

Herbicide	Application timing	Dose (g a.e./ha)	Efficacy (% Control)	Remarks
Glyphosate (IPA salt)	Early flowering	3600	~90%	High efficacy when applied at correct stage
Glyphosate + Tillage	Post-emergence + tillage	3600 + tillage	Higher than glyphosate alone	Integration improved long-term suppression
Rimsulfuron	Early vegetative stage	25	70-85%	Moderate efficacy; improved when combined
Metribuzin	Pre-emergence	500	60-75%	Less effective post-emergence
Sulfosulfuron	Flowering	20	60-80%	Effective against rosette and flowering stages

ECOLOGICAL INVASION AND ADAPTIVE TRAITS OF *S. elaeagnifolium* IN CONFLICT-AFFECTED GAZA STRIP

The ecological functioning of *S. elaeagnifolium* in the Gaza Strip is a fascinating example of how human intervention can promote the rapid growth of invasive plants. Originally from arid and semi-arid regions of North America, the plant has found favorable conditions in the war-torn and agriculturally devastated environment of the Gaza Strip. Anthropogenic disturbances in the form of soil degradation through military operations, abandonment of agricultural land, overgrazing and destructive land management practices have contributed significantly to the emergence and spread of this exotic weed.

As a result of conflict and the destruction of agricultural infrastructure, large areas of previously cultivated land were left uncontrolled, providing a perfect ecological niche for *S. elaeagnifolium*. Adaptation to impoverished soils, drought tolerance and the ability to resprout from deep root systems make the plant exceptionally resilient in such stressed environments. These environmental characteristics combined with human dispersal (e.g., through the transport of contaminated soil, equipment, or feed) have favored its spread.

The ecological success of *S. elaeagnifolium* in the Gaza Strip is an interesting example of the role of human assistance in the rapid spread of invasive species. Native to the arid and semi-arid regions of North America, the species has found a favorable environment in the war and agriculture-ravaged landscape of the Gaza Strip. Anthropogenic disturbances in the form of soil degradation caused by military activities, abandonment of agricultural land, overgrazing and destructive land management have contributed significantly to the definition and spread of this exotic weed.

The control of *S. elaeagnifolium* in the Gaza Strip is associated with numerous challenges. Mechanical and chemical control measures have limited success because the plant's root system is broad and deep, which encourages regeneration even when physically excavated or chemically treated. In addition, the blockade and limited availability in Gaza restrict access to modern control equipment. This situation calls for an integrated approach to weed management that starts at the local level and focuses on prevention, early detection, community monitoring and research into sustainable control methods such as biological control through natural enemies and allelopathic plants. Public awareness and cooperation between agricultural institutions, nature conservation authorities and researchers are urgently needed to minimize the environmental risk of this weed.

Ecological restoration of damaged habitats and regeneration of native vegetation can also limit the spread of *S. elaeagnifolium* in the long term. Future research needs to address the ecological interactions of *S. elaeagnifolium* with the native flora and fauna of Gaza, its allelopathic effect and the long-term impact of its dominance on soil diversity and health. These traits include morphological plasticity, reproductive strategy, and aboveground biomass accumulation, all of which significantly influence its success in colonization and its competitive displacement of native flora (Balah and Hassany 2023). Traits such as shoot density, stem height, and leaf length exhibited high variability depending on habitat conditions, allowing *S. elaeagnifolium* to adapt and thrive in both disturbed (agricultural and urban) and semi-natural environments (Adjim and Kazi-Tani 2018). In particular, increases in shoot density and stem elongation were positively correlated with stronger ecological impacts, such as the reduction of native plant richness and cover, especially in semi-natural and natural habitats where competition for light and space is more intense (Qasem et al. 2019).

The reproductive strategy of *S. elaeagnifolium* further amplifies its invasiveness. Its capacity to produce a large number of fruits and seeds boosts propagule pressure, facilitating rapid population establishment (Chavana et al. 2021). In disturbed habitats, this high reproductive output correlates with increased ground cover and a greater likelihood of excluding native species. These reproductive traits, combined with vigorous vegetative growth, enable the species to dominate ecosystems over relatively short timeframes (Petanidou et al. 2018).

Moreover, aboveground biomass and stem height were shown to be reliable predictors of ecological impact (Xu et al. 2020). As these traits increase, so does the plant’s competitive dominance, often leading to a significant decline in native biodiversity. Notably, the strongest impacts were not always observed in the most disturbed environments; rather, semi-natural and even natural habitats experienced considerable disruption when *S. elaeagnifolium* reached high biomass levels. These findings suggest that the plant’s invasive potential is not solely tied to disturbed conditions, but also to its ability to exploit and modify a wide range of ecological niches (Wolkovich and Cleland 2014). Overall, the trait-impact relationships elucidated in this study offer critical insight into the mechanisms driving the success of *S. elaeagnifolium* as an invasive species. Understanding how specific morphological and reproductive traits contribute to its ecological dominance provides a foundation for developing more targeted management strategies aimed at mitigating its spread and preserving native biodiversity in vulnerable habitats (Table 13).

FUTURE OUTLOOK FOR THE GAZA STRIP CONTEXT, PERSPECTIVES ON INVASION BIOLOGY AND BIORESOURCE UTILIZATION

The biofunctional properties of *S. elaeagnifolium* present promising opportunities in the Gaza Strip for health, and agro-industrial sectors. With appropriate risk mitigation, standardized extracts could serve in low-cost phytotherapeutic formulations, dietary supplements, and even bio-pesticides. However, toxicological risks require public awareness, labeling protocols, and integration of regional dietary data in pharmacokinetic models. Future local research should focus on cultivation feasibility, sustainable harvesting, and bio-based applications tailored for resource-limited contexts like Gaza Stip.

This review presents *S. elaeagnifolium* as a biologically rich but ecologically invasive species with dual potential: both as a source of pharmacologically active compounds and as an invasive threat plant. Although several studies have demonstrated its bioactive potential, particularly its antioxidant, anti-inflammatory and cytotoxic effects, there is considerable variation in the literature regarding its safety limits, toxicity profiles and therapeutic potential. While some research supports the plant's potential for drug development, other publications warn of its toxicity at higher doses and point to a narrow therapeutic window that requires rigorous validation. Ecologically, *S. elaeagnifolium* has a great plasticity and regenerative capacity that allows it to thrive in disturbed and semi-arid environments. The reasons why it became invasive, especially in regions such as the Gaza Strip, are still unknown. Comparative ecological and genetic analyzes between invaded and native populations may shed light on the adaptive traits responsible for the rapid spread of the species. From a bioresource utilization perspective, future studies need to reconcile the therapeutic properties of the plant with its ecological threat. The use of phytotherapeutics from *S. elaeagnifolium* must be accompanied by environmental management in order not to exacerbate biodiversity loss in fragile ecosystems. In addition, rigorous clinical evaluation, standardization of extracts and conservation planning are crucial to ensure safe and sustainable use of this species. Further research should focus on local pharmacological research in the Gaza Strip, such as clinical and in vivo validation of locally used preparations.

In addition, in-depth ethnobotanical surveys should be conducted to document local knowledge on preparation methods, dosage, and therapeutic applications of the plant in Palestinian communities. At the same time, regional invasive species management programs should be developed to detect, control, and possibly contain the spread of the plant, especially in pastoral and disturbed urban areas. Addressing current knowledge gaps, understanding conflicting findings, and integrating ecological and pharmacological perspectives are essential for transforming *S. elaeagnifolium* from an invasive threat into a regulated bioresource of therapeutic promise.

In conclusion, *S. elaeagnifolium* is a dual threat in the Gaza Strip both as an ecological invader and a promising bioresource. Its aggressive spread is driven by its deep root system, rhizomatous clonal growth, and allelopathic effects, which allow it to dominate degraded, post-war, and semi-arid ecosystems, displacing native vegetation and diminishing biodiversity. Despite its invasive nature, *S. elaeagnifolium* holds significant pharmacological potential, with bioactive compounds demonstrating antioxidant, antimicrobial, and anti-inflammatory properties.

Table 13. Summary of traits contributing to invasiveness and therapeutic potential

Trait category	Key traits
Invasiveness	• High crude fiber and low moisture content in leaves and flowers support drought adaptation and survival in arid Gaza Strip conditions. • Accumulation of allelopathic polyphenols suppresses neighboring plant growth and seed germination. • Presence of bioactive saponins and steroidal alkaloids deters herbivores and reduces grazing pressure, giving the plant a competitive advantage. • Efficient uptake and storage of key minerals (e.g., potassium, calcium, magnesium) even in nutrient-poor soils enhances ecological plasticity. • Bioactive compounds may serve dual ecological roles (defense and competition), explaining wide distribution in disturbed and overgrazed lands.
Therapeutic value	• Steroidal alkaloids show anticancer, antimicrobial activity. • Flavonoids (quercetin, kaempferol) contribute antioxidant and anti-inflammatory effects. • Terpenoids and essential oils and anti-inflammatory properties. • Essential oils and fatty acids show cytoprotective and antimicrobial roles. • Phenolics contribute to antiglycation and enzyme-inhibition effects. • Saponins display enzyme-modulatory, cytotoxic, and molluscicidal activity; important for future pharmacological targeting.

However, the toxicity of its glycoalkaloids calls for caution in its use for medicinal purposes. This underscores the need for safe preparation protocols, correct identification, and regulated dosage. Given this, an integrated management strategy is crucial, one that balances ecological control with the potential for medicinal applications. It is vital to consider biocontrol methods and evaluate allelochemicals for their possible role in phytoremediation and ecological restoration efforts. Furthermore, regional research should prioritize local phytochemical trials to ensure the safety and efficacy of compounds for medicinal use, particularly in resource-poor areas. Conservation strategies must integrate environmental control measures with the regulated medicinal use of *S. elaeagnifolium*, ensuring that sustainable harvesting practices and community-based cultivation are encouraged. This will not only support local economic development but also provide a sustainable source of bioactive compounds for phytomedicines, aligning with the goals of bioeconomy and health resilience in Gaza Strip and other semi-arid regions. Raising local awareness, documenting indigenous knowledge, and involving communities in cultivation practices will be key steps in balancing the ecological risks of the plant with its medicinal value, paving the way for a bioeconomic solution.

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