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ORIGINAL ARTICLE

The relationship between Invasive Alien *Solanum elaeagnifolium* Cav. characters and impacts in different habitats

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Abstract

Invasive alien plants are one of the most serious threats to agriculture. The growth traits of *Solanum elaeagnifolium* Cav. in crops and their demographics in invaded vs non-invaded communities were examined. The majority of *S. elaeagnifolium* germination was observed in the spring compared to the summer. Five stages were distinguished, which started with a short time of seedling and juvenile stages, extended flowering, and fruiting stages, and seed dispersion in the winter season. An increase in shoots/roots ratio, leaf area ratio and leaf mass fraction during growth with the varied rate was proved. The accumulation coefficient of dry mass exceeded 0.93 and was significant ($P > 0.001$) with great variability within plant parts, and stage intervals. While the high growth rate is influenced by the stages and habitats. The recipient communities are affected negatively by *S. elaeagnifolium* invasion which is associated with lower diversity, richness, and evenness vs non-invaded communities. High similarities were found in the invaded area and communities. Finally, high and varied growth and plasticity of *S. elaeagnifolium* characterized their invasion behavior via different habitats. There were suitable determinants indices of diversity that can be used in the comparison between invaded and non-invaded communities. This knowledge may be useful for use in agro-environment protection and to improve the management methods of invasive alien species.

Keywords Ecological parameters · Growth traits · Invasive alien plants · Phenology

Introduction

Biological invasions are worldwide threats causing ecological, environmental, and economic problems (Weber and Li 2008). Invasive alien plant species pose a serious threat to native ecosystem structure and function (Li et al. 2014). Ecosystem properties can be affected by invasive alien plants (Teixeira et al. 2020) and displace crop species (Wardle et al. 1994). On the other hand, the invasion is controlled by the characteristics of the invaded habitat (Sakai et al. 2001). Invasive weeds in pastures reduce forage quality and yield, impair animal performance, and increase management costs (DiTomaso 2000). While ecologists and land managers have difficulty predicting which species will become invasive (Mack et al. 2000; Kolar and Lodge 2001), the knowledge of invasive plant species biology is necessary to facilitate their management (Chauhan and Johnson 2010).

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Silverleaf nightshade (*Solanum elaeagnifolium*) is an invasive perennial species that originated from North, Central, and South American origin (Henderson 2001), invaded virtually all continents over the past century (Boyd et al. 1984), the Mediterranean basin and Europe (Mekki 2007). It invaded some cultivated areas on the North coast of Egypt (Täckholm 1974; Boulos 2009; Balah 2011) and caused in cotton, grain sorghum, wheat, and lucerne high economic losses (Boyd and Murray 1982; Lemerle and Leys 1991). It is an alternative host for phytophagous insects and plant diseases (Heap and Carter 1999; Qasem 2014). This weed injured crops, causing up to 75% yield loss, as well as an indirect impact by harboring plant pests and diseases (Uludag et al. 2016).

Invasiveness can be related to several traits: copious production of sexual and asexual propagules, the facility for long-distance dispersion, the capacity to tolerate considerable drought, and resistance to herbivory, specifically, toxicity to cattle (Mekki 2007; Scaldaferro et al. 2012). *Solanum elaeagnifolium* reproduces sexually (Cooley and Smith 1972), which has a massive seed production and different phenotypic plasticity, which could explain their different adaptation and invasiveness

in habitats with different water availability (Travlos 2013). Seeds of this weed are dispersed by animal faces, water, machinery, and agricultural products (Boyd et al. 1984), which are viable for at least six years (Stanton et al. 2011). Furthermore, it reproduces by root fragments and creeping lateral roots (Fernandez and Brevedan 1972; Cuthbertson et al. 1976). Whereas, vegetative reproduction was one of the best indicators of invasiveness among woody plants (Reichard 1994). Silverleaf nightshade growth and reproduction were affected significantly by the time of emergence (Zhu et al. 2013a), while, their distribution pattern was affected by soil moisture and rainfall (De Aparicio and Difrieri 1958). It grows on a range of soils although there is some preference for lighter, sandy soils low in organic matter (Heap and Carter 1999). This weed thrives in disturbed areas, specially cultivated and denuded areas (Wassermann et al. 1988). Generally in human-disturbed environments with no or lose tree canopy (Ganatsas et al. 2012; Formozis et al. 2021). Silverleaf nightshade can tolerate relatively high summer temperatures (20–34 °C), low annual rainfall (250–600 mm), saline soil conditions and drought-tolerant (Brunel 2011; Garcia-Fortea et al. 2019; Balah et al. 2021), which explains largely the success of its development in semi-arid bioclimatic zones (Adjim and Tani 2018). Morphological plasticity, adaptability, and a high level of genetic diversity within and between populations are partly explain the establishment and continuing expansion of *S. elaeagnifolium* (Dekker 1997; Hawker et al. 2006; Zhu et al. 2013b). The abilities of competitive and adaptations as well as spread quickly are traits correlated with invasiveness which makes invasive species very difficult to control (Willis et al. 2010; Wolkovich and Cleland 2014; Tsaballa et al. 2015; Qasem et al. 2019).

Weed surveys are useful for determining the importance of weed species (Thomas 1985). The diversity indices (Simpson and Shannon-Weiner) were useful to assess the shift in the weed population (Cardina et al. 1991). Species entrance into cropped land is mainly governed by the dynamic between habitats that function as a source of species (Williamson 1996). Therefore, the ecological characteristics within plant taxa relate to invasiveness in a particular geographic region (Richardson et al. 1989). Plant invasions often cause reductions in native species richness and overall biodiversity (Hansen et al. 2020). Species abundances are more likely to interact with newly introduced species (Thuiller et al. 2010). The richness decreased in invaded compared to non-invaded localities (Hejda et al. 2009). Whereas, resident plant evenness may be important in suppressing weed invasion into grassland communities (Wilsey and Polley 2002; Tracy and Sanderson 2003).

The study hypothesized that the growth rate of *S. elaeagnifolium* differed among the crops, localities and seasons due to their plasticity. Also, their ecological impacts can differentiate clearly from the diversity indices via a comparison of invaded vs. non-invaded resident communities, whereas, there were more suitable diversity indices than others for studying this task. The objectives were to study the phenological traits and developmental growth of *S. elaeagnifolium* in invaded crops and non-invaded communities. Surveillance data about the species relative abundance, diversity and evenness, as well as the coefficient of similarity among localities were provided. This knowledge is relevant for promoting prevention methods for invasive weed agro-ecological problems and control efforts.

Materials and methods

Growth trials of *S. elaeagnifolium*

The study sites were conducted in the infested area at Borg al-arab in south-west Alexandria and El-Hammam in an eastern area in Matruoh governorates on the north coast of Egypt from 2017 to 2020. These areas are characterized by a moderate climate with average temperatures between 18–30 °C, rains above 50 mm in winter, and average relative humidity of approximately 65% per year. The soil was a sandy loam to loamy sand according to FAO – UNESCO methods and Soil Taxonomy (FAO – UNESCO 1971–1981), with, pH 8.2 and 8.4 and electrical conductivity of 0.819 and 0.854 ds /m in Borg al-arab and El-Hammam respectively. The soil contains the following anions; (1.912 meq/l l) sodium, (1.23 meq/l) potassium, (2.55 meq/l) calcium and cations by (2.39 meq/l) HCO3, (1.98 meq/l), chloride, (2.18 meq/l) sulfate, respectively. The seedling growth of *S. elaeagnifolium* was observed regularly during the visits to wheat, faba bean, and Egyptian clove crops in winter and sesame, maize in summer, gapes, fig and uncultivated lands over the year. Some plants were marked to determine their age. The studied weed was collected and sorted at different stages, whereas, the numerical phenology ratings were given to phenophases; 1 = seedling, 2 = juvenile, 3 = flowering, 4 = fruiting, and 5 = seed dispersal according to the phenological index technique of West et al. (1971).

Another experiment was conducted in pots to investigate the germination and growth during the year under different environmental factors than their current spreading environment. The plastic pots filled with the same sandy loam soil and placed outdoors (outside the laboratory). The seeds were sown every month at a depth of 0.5 cm after soaking in running water for 24 h to remove the mucilage. The pots

were watered at regular intervals. The average temperature during experiments was ranging from 20 to 35 °C. Five pots per harvest regularly after 15, 30, 60, and 90 days to determine the growth rates. To analyze the change in germination rate or germinability during the year, 5 pots were sowed every month, each pot containing 5 seeds. The number of germinated seeds was counted once at the end of the month (four weeks), then the germination percentage was calculated.

Ten plants were collected per life stage from each tested crop and sectioned into roots, shoots, leaves, fruits, and whole plants. These tissues were dried for 24 h at 80 °C and weighed. Numbers of leaves, flowers and branches were recorded. Leaf area per plant was measured with a leaf area meter (C1-203 handheld laser area meter CID, Inc. made in USA).The data of dry mass weight via the time [days from emergence (DFE)] were transferred to natural logarithms for fitting to polynomial regression equations. Plant traits such as leaf area ratio (LAR = plant leaf area/plant mass), root/shoot ratio (R/S ratio, the ratio of root biomass to shoot), leaf mass fraction (LMF = Leaf dry mass / Total plant dry mass), root mass fraction (RMF = Root dry mass / Total plant dry mass), stem mass fraction (SMF = Stem dry mass / Total plant dry mass), specific leaf area (SLA = Leaf area / Leaf dry mass), specific stem length (SSL = Stem length/ Stem dry mass) were determined. Relative growth rate (RGR) is calculated as RGR = (ln W2 – ln W1) / (t2 – t1), where W1 and W2 are dry weights at times t_1 and t_2 as described in Cornelissen et al. (1996). Net assimilation rate is defined as the rate of increase of dry weight (W) per unit of leaf area (L) for each time-interval (t_2–t_1) according to (Gregory 1926) from the formula;

$$NAR = \frac{(W2 - W1)(logeL2 - logeL1)}{(t2 - t1)(L2 - L1)}$$

The values for growth were derived from the regression coefficients using the general formula for a second-order polynomial equation f = (y0 + a * x + b * x^2 + c * x^3) derived from the relationship between; F is the phenotypic trait value, y0 are fixed effects of the overall intercept, (a), (b), and (c) are fixed components of the model, x is the weights variable. The phenotypic plasticity index is according to the following formula: IPF = (value of maximum mean – value of minimum mean) / (value of maximum mean) for each trait (Valladares et al. 2000).

Floristic analysis

The flora surveys were conducted between the years 2017 to 2020 in Borg al-arab and El-Hammam areas of Egypt. These studies have monitored a total of 320 samples (160 and 160) of invaded and non-invaded sites respectively (including 20 samples from each crop or rangelands) that were chosen adjacent to each other in each crop and season to represent (maize and sesame) summer and (wheat, faba bean and Egyptian clover) winter crops as well as (fig, grape) fruits (to represent most invaded crops) and rangelands. The number of species or individuals and the total weeds in m^2 were counted in a random pattern according to (Thomas et al. 1997). Weeds were counted within quadrates of 100 lengths X 1 m^2 wide and taken randomly to assess the individual species densities. Data were summarized by relative abundance (RA) value; the sum of the individual relative frequency (frequencies % divided by the total number of all frequencies), relative field uniformity (the percentage infestation of the field by the species of interest to the surface area occupied by the weed) and relative field density percentages (main field density of k species divided by sum to main field density of all species multiplied by100) according to (Thomas 1985).

1 Relative frequency for species k

$$RFk = \frac{\text{Frequency value of species k}}{\text{Sum of frequency value for all species}} \times 100$$

2 Relative field uniformity for species k

$$RFU\ k = \frac{\text{Field uniformity value of species k}}{\text{Sum of field uniformity value for all species}} \times 100$$

3 Relative mean field density value of species k

$$RMFDk = \frac{\text{Main Field Density value of species k}}{\text{Sum of mean field density value for all species}} \times 100$$

4 Relative abundance RA value for species k

$$RA_k = RF_k + RFU_k + RMDF_k$$

Importance value (IV) = Relative cover (RCi) + Relative density (RDi) + Relative frequency (RFi). Sorenson coefficient of similarity was used to measure the similarity of species compositions between the invaded and non-invaded areas within the localities and seasons (Newsome and Dix 1968) obtained from = [2C / (A + B)] × 100 where C = number of species in common, A = total number of species in the first area and B = total number of species in the second area. The diversity was measured by the Simpson dominance index to characterize species diversity in a community through uniform of species distribution, Shannon-Wiener diversity index to describe the disorder and uncertainty of individual species according to (Smith and Wilson 1996; Shannon and Weaver 1949), richness index (Margalef 1958) and measures species evenness (J') which related to individual distribution according to (Pielous 1975) by Pielou's index (E1), Sheldon's index (E2), Heip's index (E3), Hill's index (E4), and Modified hill's ratio (E5) to give more information about these communities (Simpson 1949).

Data analysis

The difference among the mean germination values and months were determined by ANOVA, as well as other traits (lengths, leaf numbers, leaf area, leaf weight, main stem weight, root weight and total dry weight) and phenology stages, while the interspecific comparison between growth stages and hast crops were performed using two way A nova using statistical package of SPSS IPM 19 (IBM Corp. Armonk, NY, USA) by Tukey's test to examine the differences between growth in different stages. Polynomial regression equations were prepared using SigmaPlot software v.12.5 (Systat Software Inc., CA, and USA) of dry weight accumulation per stage.

Results

Phenology of *S. elaeagnifolium*

The differences in main germination values and months were significant ($F = 117.345$, $p \leq 0.00$) (Fig. 1). The seed germination was recorded in the spring and summer seasons and the maximum germinability was recorded mainly in March (63.5%) and April (63.8%), respectively. However, there was a remarkable decrease from October (20.05%), November (16.67%), to reach the minimum germination in December (6.33%) and January (6.37%), respectively.

The phenological of *S. elaeagnifolium* was distinguished by five life stages as follows: seedlings emerge quickly after germination, followed by a juvenile stage that occurs in the winter, spring, and early summer, and then a lengthy flowering stage that occurs in the spring, summer, or autumn seasons. The majority of flowering occurred from May to September and is prolonged to November. While, the matured fruits started with few numbers from April to July, the majority of the matured fruits were found from August to November. Lastly, in the winter season, most of the seed dispersion occurred from December to next February or later if the plant did not remove. *S. elaeagnifolium* life cycle has a wide range of 40 to 90 days with an average of 65 days to transform from emergence to produce matured fruits depending on the condition and habitats (Fig. 2).

In general, *S. elaeagnifolium* growth is very rapid in spring and summer as compared with the growth in autumn seasons and there was a gradual increase of phytomass dry weight from the seedling to the final stage at different rates. The plant growth and development were significantly increased over the times ($F = 66.91$, $p \leq 0.00$) lengths, ($F = 19.94$, $p \leq 0.00$) leaf numbers. ($F = 891.182$, $p \leq 0.00$) leaf area, ($F = 59.09$, $p \leq 0.000$) leaf weight, ($F = 110.77$, $p \leq 0.000$) root weight, ($F = 117.73$, $p \leq 0.000$) stem weight, ($F = 93.45$, $p \leq 0.000$) of total dry weight, respectively. Likewise, the ratio of shoots/ roots increased. The ratio of leaf area and leaf mass fraction has highly increased from the seedling stages until the flowering stage and slightly to the end (dispersal stages). Root mass fraction, stem mass fraction, specific leaf area and specific stem length have been steadily reduced. High growth plasticity was observed in the measured traits which reached the optimum (0.985) in total dry mass and specific leaf mass fraction (0.899) respectively. However, minimum plasticity values were detected in stem mass fraction, shoot to root ratio and leaf area ratio (Table 1).

Relative growth rate and net assimilation

The relative growth rate (RGR) of *S. elaeagnifolium* was important as a key for growth measurement and competition with other plant species. The maximum RGR observed in the seedling–juvenile interval and develops slowly during the juvenile-flowering interval, then develops with a small rate at the remaining flowering and fruiting growth intervals. The relative growth rate of *S. elaeagnifolium* was higher

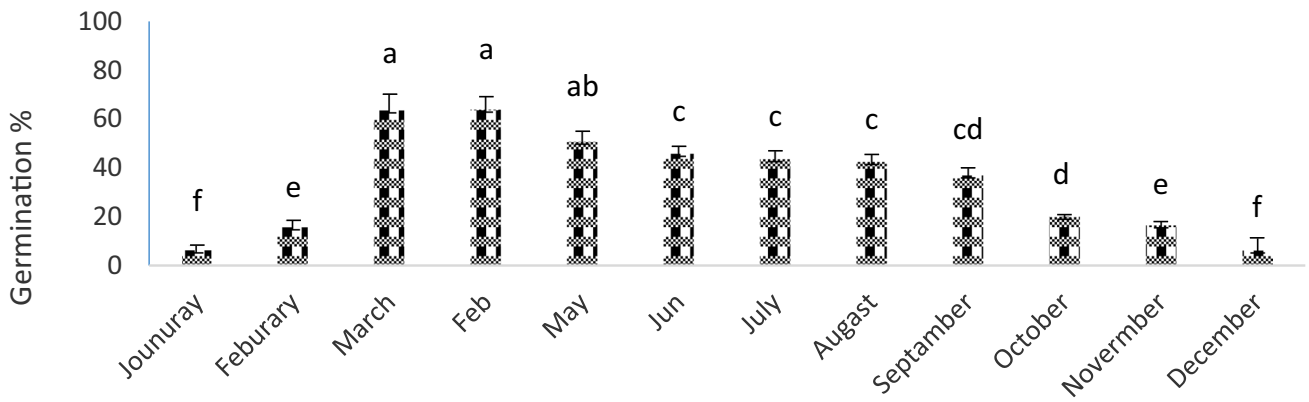


Fig. 1 Germination percentage of S. *elaeagnifolium* during the year

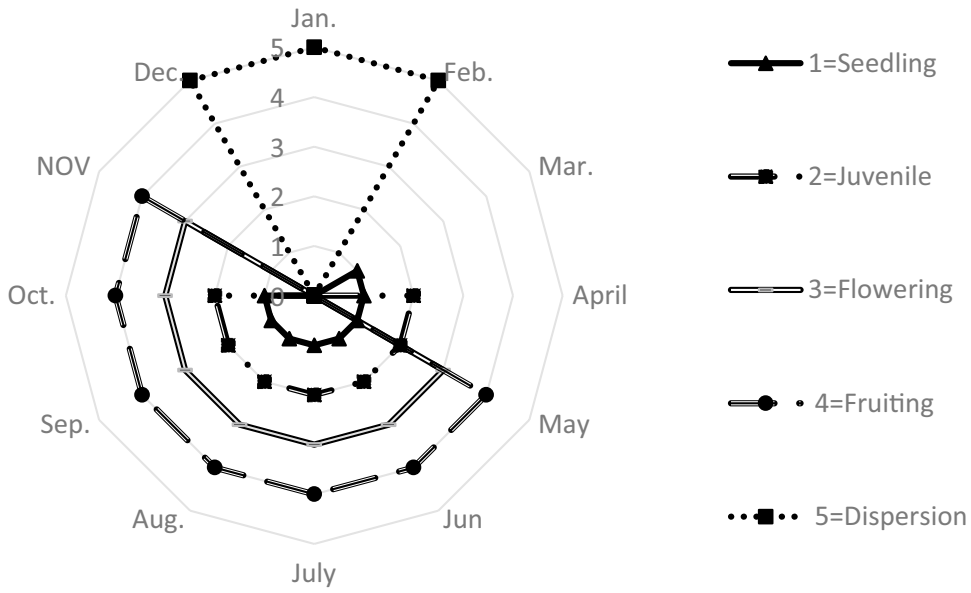


Fig. 2 Life stages of *S. elaeagnifolium*; 1 = seedling, 2 = juvenile, 3 = flowering, 4 = fruiting, and 5 = seed dispersal

Table 1 The growth traits of the leaf area ratio (LAR), Leaf mass fraction (LMF), Root mass fraction(RMF), Stem mass fraction (SMF), Specific leaf area (SLA) and specific stem length (SSL) over the phenology stages

Stages	Total dry mass (g)	Shoot to root ratio (g g-^{1})	Leaf area ratio (Kg/m^{2})	Leaf mass fraction (g g -^{1})	Root mass fraction (g g -^{1})	Stem mass fraction (g g -^{1})	Specific leaf area (m^{2} kg^{-1})	Specific stem length (cm kg^{-1})
Seedling	0.29 ± 0.38	0.86 ± 0.06	2.21 ± 0.30	0.074 ± 0.006	0.300 ± 0.02	0.258 ± 0.03	29.59 ± 3.48	80.74 ± 6.11
Juvenile	4.87 ± 0.27	1.05 ± 0.12	1.36 ± 0.05	0.028 ± 0.001	0.139 ± 0.01	0.147 ± 0.012	48.44 ± 1.72	35.78 ± 2.79
Flowering	10.37 ± 0.43	1.61 ± 0.063	1.303 ± 0.06	0.014 ± 0.001	0.162 ± 0.01	0.262 ± 0.01	129.30 ± 9.35	15.28 ± 1.26
Fruits	16.51 ± 1.25	1.65 ± 0.09	1.21 ± 0.10	0.009 ± 0.001	0.169 ± 0.02	0.279 ± 0.02	138.45 ± 10.08	13.78 ± 1.46
Seed dispersing	19.39 ± 1.54	1.70 ± 0.02	1.11 ± 0.12	0.007 ± 0.001	0.166 ± 0.02	0.283 ± 0.02	149.13 ± 15.78	13.59 ± 1.46
Plasticity index (IPF)	0.985	0.494	0.494	0.899	0.537	0.481	0.802	0.832
F (P values)	206.9(0.00)	12.57(0.017)	62.38(0.00)	3.66(0.023)	3.15(0.043)	2.57(0.100)	250.8(0.000)	180 (0.000)

in summer than in winter and in rangelands than in fruit fields. However, it was lower in winter crops than in other tested crops (Fig. 3). The differences in *S. elaeagnifolium* growth of total dry weight were significant (F = 108.56, $p \leq 0.00$) among crop types, (F = 47.69, $p \leq 0.00$) life stages, and (F = 2.69, $p \leq 0.03$) seasonal crops respectively. The interaction effect in *S. elaeagnifolium* of total dry weight was significant (F = 3.082, $p \leq 0.00$) between crop types and life stages, however, this interaction was insignificant (F = 1.03, $p \leq 0$ 0.47) between seasonal crops and crop types and (F = 0.76, $p \leq 0.065$) between seasonal crops and stages of total dry weight.

The net assimilation rate (NAR) is associated with photosynthetic and respiration rates. It increased significantly over the stages (F = 1417.8, $p \leq 0.00$) seedling, (F = 2,356,717.7, $p \leq 0.00$) juvenile, (F = 4,385,821.8, $p \leq 0.00$) flowering, (F = 1,908,451.9, $p \leq 0.000$) fruiting respectively. The NAR was observed greatest in the flowering stages and reaches the maximum in grapes followed by Figs. However, it was low in wheat and Egyptian clover crops. In general, NAR of *S. elaeagnifolium* appeared high in the summer season, fruit crops and rangelands (Fig. 4).

The relationship of *S. elaeagnifolium* biomass accumulation and times from days of emergence to the final stage has been described by polynomial regression equations (Table 2). This accumulation indicated the plant performance from stage to stage and from time to time under various conditions. The coefficients of determination exceeded 0.93 and the cubic term was significant ($P > 0.001$). Plant dry matter exhibited great variability within plant parts and between the harvest intervals. While the overall accumulation of biomass has varied between crops, it was higher in sesame and figs than in other crops. The interaction effects of *S. elaeagnifolium* growth traits

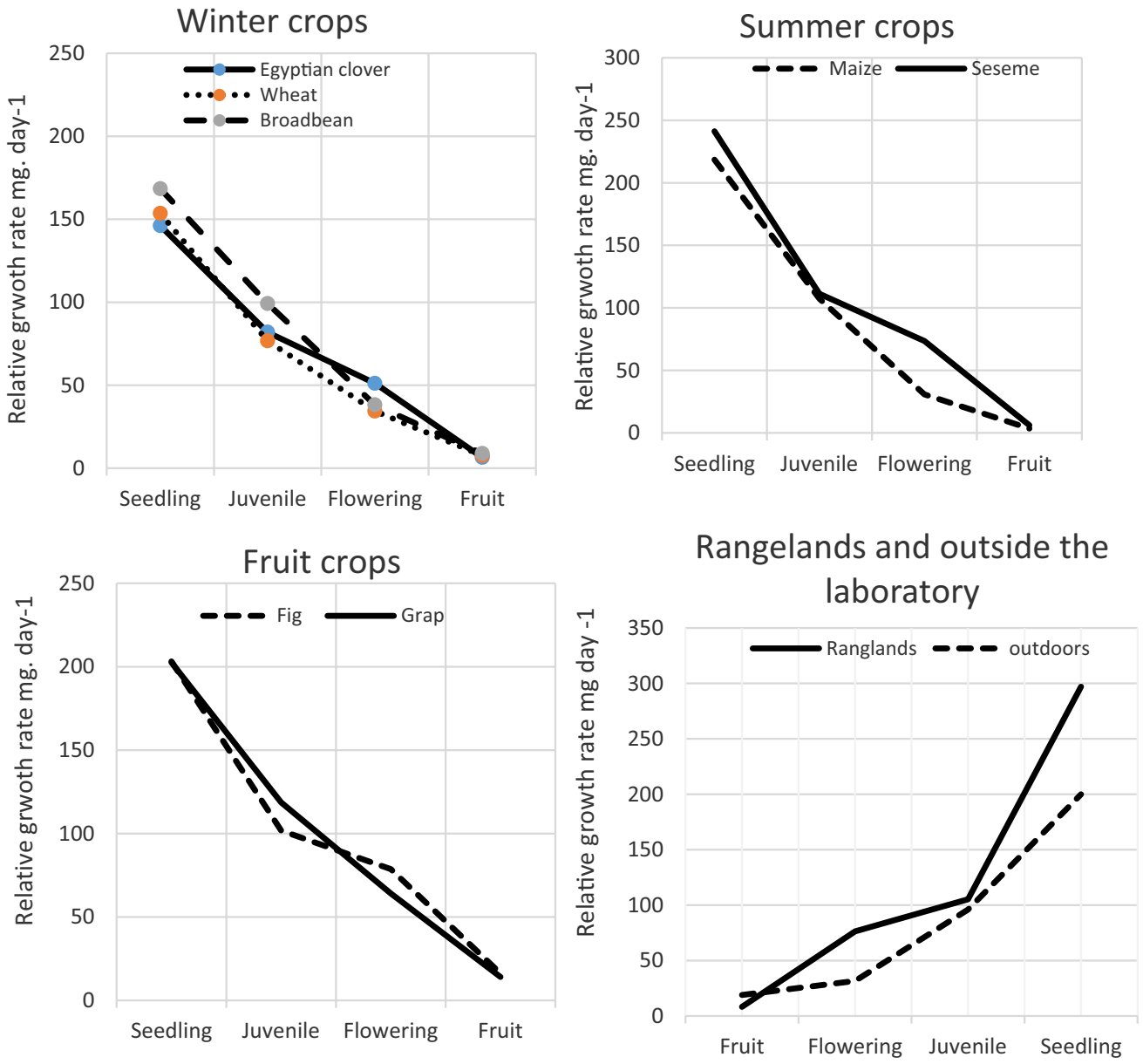


Fig. 3 Relative growth rate of *S. elaeagnifolium* during growth stages in different habitats

among different crops and stages were significantly (F=262.7, $p \leq 0.00$) root, (F=392.1, $p \leq 0.00$) stem, (F=346.3, $p \leq 0.00$) leaves, (F=787.2, $p \leq 0.000$) fruits and (F=3135, $p \leq 0$ 0.00) total plant of dry weight respectively.

Floristic analysis of areas and seasons

The floristic analysis was conducted in the adjacent areas of *S. elaeagnifolium* invaded and non-invaded sites. The mean percent of *S. elaeagnifolium* invaded lands ranged from 31 to 37% (Borg al-arab) and 25 to 28% (El-hammam) of the cultivated lands respectively. A total of 33 species were found belonging to 30 genera within 14 families in these areas. Regarding non-invaded sites, the number of species was 33 species (Borg Al-arab) and 30 (El-hammam), 21 (winter) and 19 (summer) respectively. While in the invaded areas, the number of species including 30 species (Borg al-arab) and 27 (El-hammam), 18 (winter) and 14 (summer) respectively. The highest number of species was found in the family Poaceae, followed by Brassicaceae. The recorded species in the studied communities were *Sonchus oleraceus* L., *Xanthium stramonium* L., *Conyza linifolia* (Willd.) Täckh., *Amaranthus retroflexus* L., *Sisymbrium irio* L., *Silybum marianum* (L.) Gaertn., *Sonchus arvensis* L., *Brassica tournefortii* Gouan.,

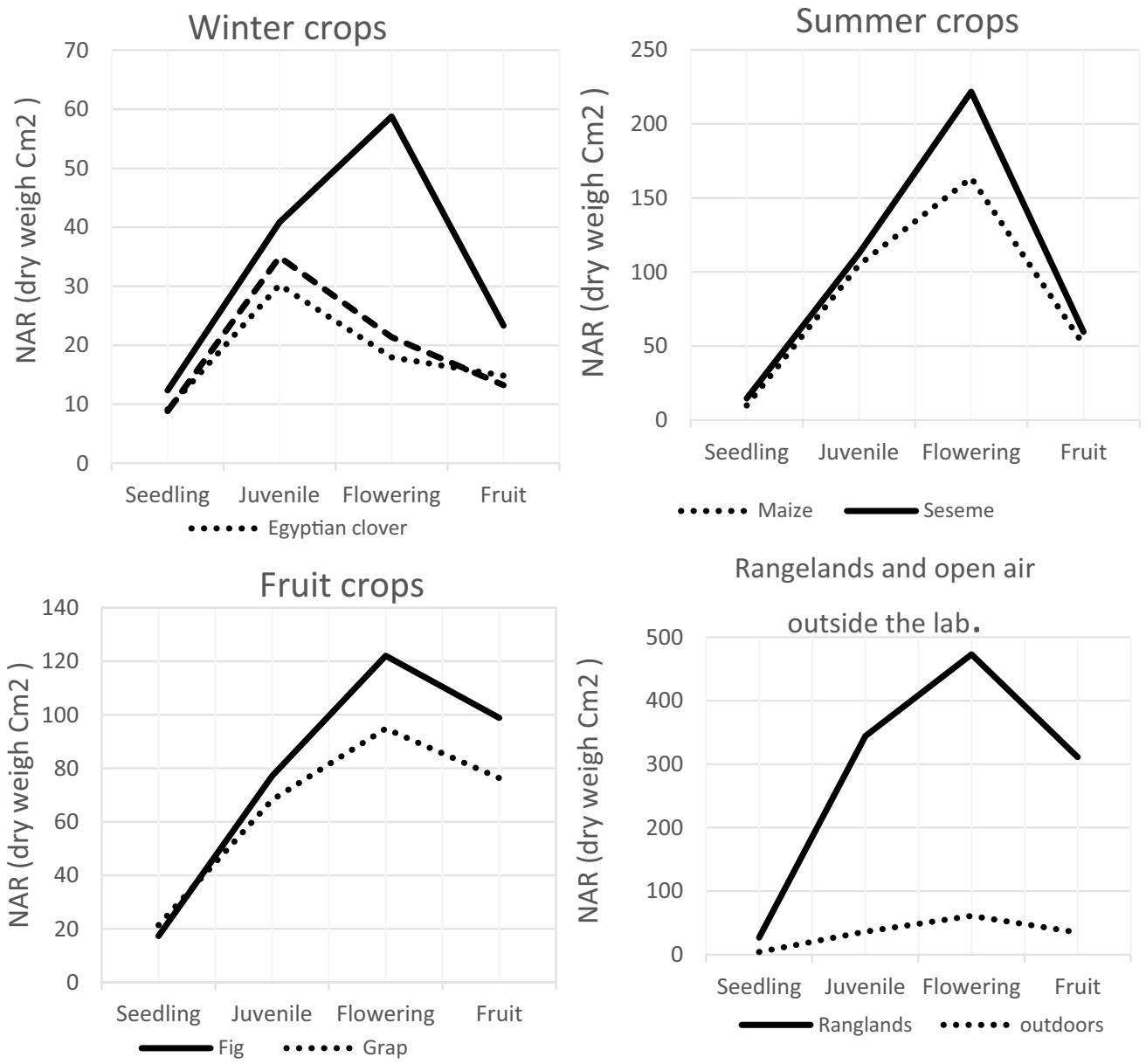


Fig. 4 Net assimilation rate of *S. elaeagnifolium* during growth stages in different habitats

Capsella bursa-pastoris (L.) Medik., *Beta vulgris* L., *Chenopodium album* L., *Chenopodium murale* L., *Cichorium endivia* L., *Lathyrus hirsutus* L., *Urtica urens* L., *Amaranthus ascendens* Loisel., *Amaranthus viridis* L., *Conyza bonariensis* L., *Convolvulus arvensis* L., *Cyperus rotundus* L., *Euphorbia peplus* L., *Melilotus indica* (L.) All., *Medicago polymorpha* L., *Vicia sativa* L., *Malva parviflora* L., *Oxalis corniculata* L., *Rumex dentatus* L., *Emex spinosum* L., *Cynodon dactylon* (L.) Pers., *Imperta cylindrica* (L.) P.Beauv., *Poa annua* L., *Avena fatua* L., *Lolium multiflorum* Lam., *Bromus tectorum* L., *Phalaris minor* Retz., *Hordeum marinum* Huds., *Dactyloctenium aegyptium* (L.) Willd., *Setaria viridis* (L.) P. Beauv., *Cenchrus ciliaris* L., *Agropyron repens* L., *Digitaria sanguinalis* (L.) Scop., *Dichanthium aristatum* (Poir.) C.E.Hubb., *Lolium perenne* L., *Phragmites communis* (Cav.) Trin. ex Steud., *Echinochloa colona* (L.) Link, *Solanum nigrum* L., *Solanum eleaegnifolium* Cav. and *Kochia indica* Wight.. These species were belonging to *Asteraceae*, *Amaranthceae*, *Brassicaceae*, *Chenopodiaceae*, *Convolvulaceae*, *Cyperaceae*, *Euphorbiaceae*, *Fabaceae*, *Malvaceae*, *Oxalidaceae*, *Polygonaceae*, *Poaceae*, *Solanaceae* and *Urticaceae*.

In the invaded areas, *S. elaeagniflium* species had relative abundances (RA) reached 19.97 (Borg el-arab) and 30.81 (El-hammam), respectively. Followed by

Table 2 Regression equations for *S. elaeagnifolium* roots, shoots, leaves fruits, and total plant dry weights from emergence days

	Growth (mg)	Equation (f = y0 + a * x + b *x^ 2 + c *x ^3	R^2	F	P values
Egyptian clover	Roots	-47.48 + 6.9 x + 0.56 x^2- 0.004 x^3	0.935	8871.8	0.008
	Stems	17.35 - 82.51 + 6.06 x^2- 0.038 x^3	0.999	1438.5	0.000
	Leaves	62.79 - 94.5x + 6.-14 x^2- 0.004x^3	0.993	1265.9	0.000
	Fruits	----------	-----	----	---
	Total plant	-29.98 -12.16 x + 2.19 x^2- 0.017 x^3	0.991	1697.127	0.003
Wheat	Roots	-29.67 - 2.39 x - 0.8921 x^2 - 0.006 x^3	0.975	346.665	0.008
	Stems	31.99 - 102.51 x + 7.30 x^2 - 0.04 x^3	0.999	4944.022	0.001
	Leaves	-9.36 - 68.1 x + 5.54 x^2 - 0.03 x^3	0.988	3284.242	0.007
	Fruits	----------	----	----	---
	Total plant	-44.66 -11.61 x + 2.5 x^2- 0.0154 x^3	0.997	2894.6	0.006
Faba bean	Roots	-36.012 - 4.47 x + 1.20 x^2- 0.008 x^3	0.974	3375.0	0.007
	Stems	77.48 -139.8 x + 9.14 x^2- 0.1 x^3	0.988	2021.2	0.005
	Leaves	74.8 - 272.5 x + 15.12 x^2- 0.1 x^3	0.973	8797.7	0.006
	Fruits	----------	-----	----	---
	Total plant	25.95 - 61.7 x + 4.99 x^2- 0.029 x^3	0.967	5171.6	0.004
Maize	Roots	-59.37 + 5.5 x + 0.96 x^2- 0.007 x^3	0.939	97,016.3	0.000
	Stems	102.29 -168.72 x + 10.88 x^2- 0.06 x^3	0.997	43,621.0	0.000
	Leaves	-76.46 - 91.75 x + 5.5 x^2- 0.037 x^3	0.985	13,598.3	0.000
	Fruits	-39.62 + 36.4 x -2.14x^2- 0.02 x^3	0.997	38,844.4	0.000
	Total plant	-79.75 - 218.5 x + 15.18 x^2- 0.084 x^3	0.998	19,957.0	0.000
Sesame	Roots	-58.42 + 0.22 x + 1.37 x^2- 0.01 x^3	0.960	1,041,282.3	0.000
	Stems	-105.8 -168.72 x + 12.48 x^2- 0.076x	0.999	609,627.3	0.000
	Leaves	193.4 -214.9 x + 12.47 x^2- 0.084 x^3	0.981	2,495,916.9	0.000
	Fruits	-50.99 + 46.9 x -2.76 x^2- 0.03 x^3	0.997	3,757,154.2	0.000
	Total plant	-89.98 -358.1 x + 23.56 x^2- 0.134 x^3	0.992	1,645,973.5	0.000
Fig	Roots	-82.24 - 4.29 x + 2.28 x^2- 0.016 x^3	0.973	30,081,449.0	0.000
	Stems	-43.5 -178.36 x + 14.69 x^2- 0.08 x^3	0.999	1,481,934.0	0.000
	Leaves	367.7 - 387.6 x + 22.07 x^2- 0.14 x^3	0.978	3,849,367.2	0.000
	Fruits	-367.5 + 319.6 x -18.06 x^2 + 0.22 x^3	0.996	2,916,969.2	0.000
	Total plant	-119.7 + 0.533 x + 3.74x^2- 0.002 x^3	0.996	3,881,449.0	0.000
Grape	Roots	-102.27 + 0.66 x + 2.3 x^2- 0.016 x^3	0.964	975,016.3	0.000
	Stems	-134.56 -23.3 x + 7.09 x^2- 0.02 x^3	0.997	434,621.0	0.000
	Leaves	128.5 - 407.33 x + 22.19 x^2- 0.14 x^3	0.969	173,598.3	0.000
	Fruits	-349.3 + 304.22 x -17.2 x^2 + 214 x^3	0.996	366,844.4	0.000
	Total plant	-112.8 + 27.75 x + 2.18 x^2 + 0.012 x^3	0.994	195,957.0	0.000
Rangelands	Roots	-55.0 -104.06 x + 13.65 x^2- 0.065 x^3	0.998	339.7	0.002
	Stems	280.7 -53.12 x + 32.02 x^2- 0.06 x^3	0.972	444.6	0.001
	Leaves	190.75 - 581.12 x + 32.02 x^2- 0.21x^3	0.972	405.5	0.0003
	Fruits	-513.3 + 446.7 x -25.25 x^2 + 0.13x^3	0.996	631.6	0.005
	Total plant	-217.76 - 241.1 x + 23.76 x^2- 0.008 x^3	0.967	34,138.2	0.001
Outdoor	Roots	-12.86 + 1.26 x + 0.24 x^2- 0.0017 x^3	0.968	14,790.2	0.000
	Stems	-21.1 - 11.49 x + 1.46 x^2- 0.009 x^3	0.996	32,983.6	0.000
	Leaves	8.66 - 26.8 x + 1.944 x^2- 0.012x^3	0.999	34,557.6	0.000
	Fruits	----------	----------	.	.
	Total plant	-0.99 -52.46 x + 4.24x^2- 0.02 x^3	0.999	667,246.4	0.000

Silybum marianum, Cynodon dactylon and *Malva parviflora* species with RA reached 18.14, 18.56 and 15.97 (Borg el-arab) and *Hordeum marinum, Convolvulus arvensis* and *Beta vulgris* by 17.67, 17.45 and 16.54 (El-hammam), respectively. Regarding seasonal infestation, *S. eleaegniflium* had RA of 25.37 and 59.04 in the winter and the summer respectively. The highest RA species were *Chenopodium* sp. by 22.40 (winter) and *Dactyloctenium aegyptium* by 23.84 (summer) respectively. Among the non-invaded, regarding areas, the higher relative abundance was *S. marianum* and *C. dactylon* by 18.14 and 18.56 (Borg al- arab) and *Convolvulus arvensis*, *Hordeum marinum* and *Imperata cylindrica* by 17.45, 17.65 and 15.02 (El-hammam), respectively. Regarding seasonal infestation, the high RA was achieved from *Phalaris* sp. by 30.51 in winter and *C. dactylon* by 20.61 in summer respectively (Fig. 5).

In the present research, *S. eleaegniflium* was the most common weed in invaded areas, which had slightly lower richness than in non-invaded areas. The diversity indices of Simpson (λ), Shannon (H') gave the highest values for non-invaded as compared with invaded localities. Evenness indices of hill's index (E4) and modified hill's ratio (E5) were more adaptive and have the lowest value in the invaded area relative to non-invaded localities. However, Pielou's index (E1), Shannons's index (E2), Heip's index (E3) did not appear any differences between the invaded and non-invaded localities. While Shannons's indices and Simpson indices allowed better comparison between various areas, we found Evenness indices E4 and E5 have a great sensitivity for comparison between the invaded and non-invade areas, these indices refer to the greatest importance to *S. eleaegniflium* invasion (Table 3).

The coefficient of similarity (CS) of species was calculated between various areas and seasons of non-invaded and invaded sites. The CS reached 75.80% and 82.61% in non-invaded and invaded areas respectively. Whereas, it was calculated by 24.13% and 25.33% winter and summer seasons respectively. Regarding the region, it reached 92.0% (Borg al-arab : Borg al-arab) and 80.4% (El-hammam : El-hammam) respectively. As for the CS within the same season, it reached 79.4% (winter : winter) and 65.3% (summer : summer) respectively (Table 3).

In the present research, the importance value index (IV) in the invaded area pointed to *S. elaeagnifolium* as a high IV species reached 108.14 (Borg al-arab), 115.21 (El-hammam), 109.88 (winter), 129.46 (summer), respectively in the concerning communities. It has shown the second set of IVI achieved from *C. dactylon* by 90.78 (Borg arl- arab) and 71.09 (El-hammam), *Silybum marianum* by 91.87 (winter), *Portulaca oleraceae* by 77.05 (summer) respectively. Regarding the non-invaded area, the greater IV was *Cynodon dactylon* by 93.86, followed by *Convolvulus arvensis* by 75.25 (Borg al-arab), *C. arvensis* and *Cyperus rotundus* reached 73.49 and 70.06 (El-hammam area), respectively. As for seasons in non-invaded, the highest IV was *Malva parviflora* by 80.27 (winter), *Dactyloctenium aegyptium* and *C. arvensis* by 81.41, 83.39 (summer) respectively (Fig. 6).

Discussion

The growth traits of *S. elaeagnifolium* and the impacts in different habitats were illustrated which could be important for understanding its invasion behavior and helps to highlight the importance of *S. elaeagnifolium* management effectively.

The role of growth characteristics in *S. elaeagnifolium* behavior

A high growth rate of *S. elaeagnifolium* had recorded in different habitats with variation in dry matter accumulation based on the life stages. Which could be accelerated their maturity from the seedling to the fruiting stage. There was an increase in shoots/ roots ratio, leaf area ratio and leaf mass fraction across the time that reflects a better colonizing in this area. However, root mass fraction, stem mass fraction, specific leaf area, and specific stem length were reduced via time. *S. elaeagnifolium* has a wide time for germination extending from the spring to summer with the optimum in March and April. It has a rapid and wide life cycle duration (40 to 90 days) influenced by habitat environmental conditions. The short seedling and juvenile period indicated that the time available for control is very short. Perennial weeds at the 5 to 7 leaf stage of seedling or juvenile are recommended for herbicide applications (Aulakh et al. 2014). It is exhibited from a wide range of life cycles, with a high ratio of leaf area and rapid and high germination are excellent seed traits for many invasive species under stress conditions (Ye and Wen 2017). Plant-plant interaction via competitive indices, plant morphological traits, soil nutrient contents, enzyme activities, and microbial biomass are essential to weed invasion success (Xu et al. 2020). Regarding the growth analysis by regression and relative growth rate, *S. elaeagnifolium* has a higher growth rate in rangelands than in cultivated crops (Table 2). Likewise, a high relative growth rate and net assimilation were perceived in summer than in the winter season. The highest NAR was detected during the flowering stages and in the summer (Fig. 3). The potentiality of *S. elaeagnifolium* growth has an ascending order; rangelands > sesame > fig > faba

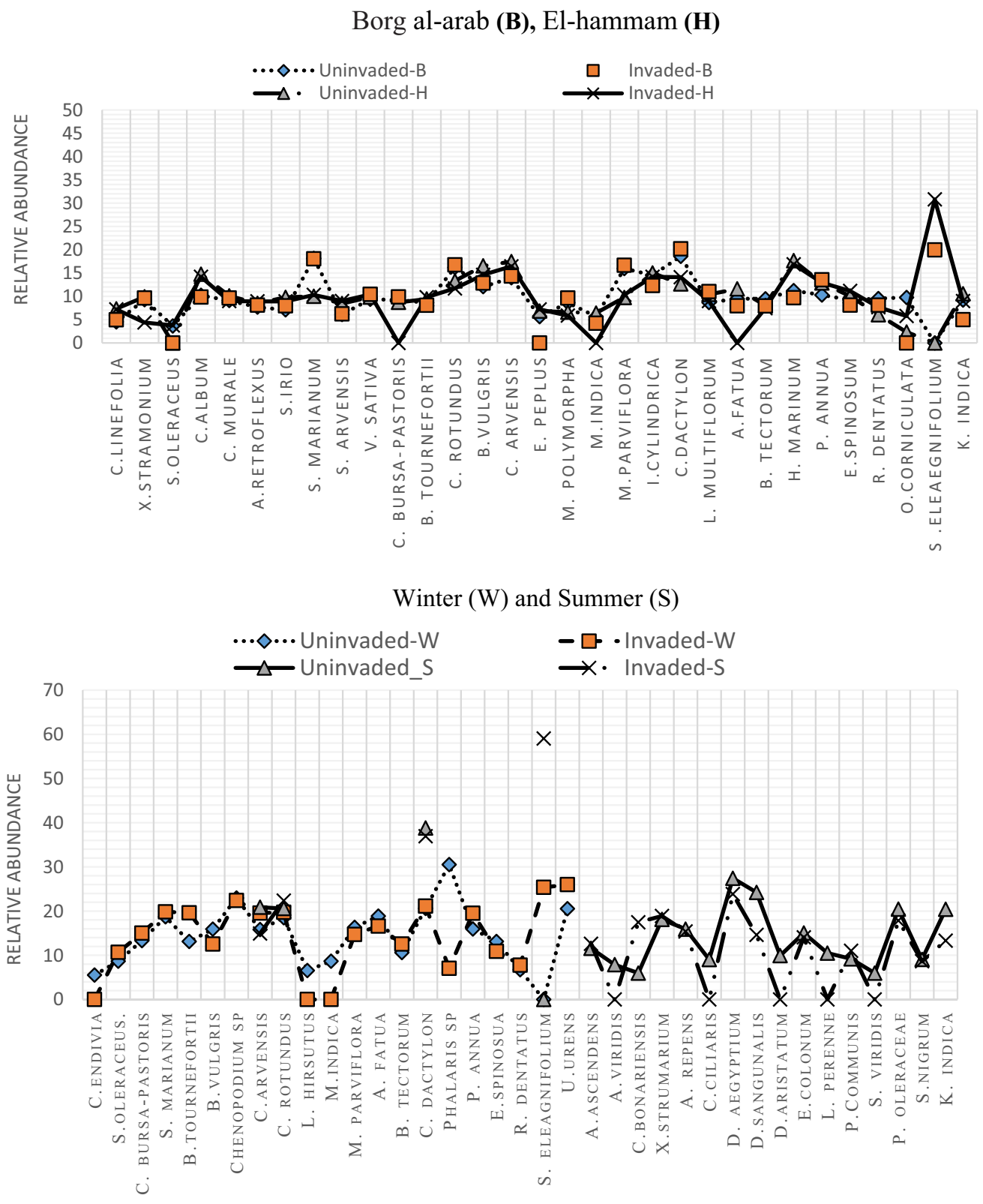


Fig. 5 Relative abundance of the surveyed species in the two areas and seasons

Table 3 Richness, similarity, diversity, and evenness of invaded and non-invaded localities of *S. elaeagnifolium*

		Uninvaded				Invaded			
		Borg al-Arab	El-hammam	Winter	Summer	Borg al-arab	El-hammam	Winter	Summer
Richness	Richness index 1 (R1)	7.19	7.06	6.37	6.71	7.150	7.04	6.36	6.62
	Richness index 2(R2)	3.56	3.43	2.67	3.04	3.51	3.42	2.59	3.01
Coefficient of Similarity *(%)		75.80%		24.13%		82.61%		25.33%	
	Winter: Winter			79.4%					
	Summer: Summer				65.3%				
	El- hammam: El- hammam		80.4%						
	Borg al- arab: Borg al- arab	92.0%							
Diversity	Simpson index1 (λ)	0.028	0.032	0.058	0.07	0.023	0.031	0.05	0.06
	Shannon index (H')	2.955	3.055	2.625	3.011	2. 894	2.897	2.605	2.682
Evenness(J')	Pielou's index (E1)	0.36	0.36	0.36	0.36	0.36	0.36	0.36	0.36
	Sheldon's index (E2)	0.11	0.11	0.11	0.11	0.11	0.11	0.11	0.11
	Heip's index (E3)	0.08	0.08	0.08	0.08	0.08	0.08	0.18	0.08
	Hill's index (E4)	9.88	8.68	4.87	3.96	6.93	5.22	3.59	2.47
	Modified Hill's ratio (E5)	13.42	11.75	6.41	5.14	9.30	6.90	4.62	3.05

bean > maize > grape > wheat > Egyptian clover. These rankings are functional to strong growth and respectable traits of *S. elaeagnifolium* which can be facilitated their establishment. Accordingly, the obtained results supported the hypothesis that *S. elaeagnifolium* high growth rate and plasticity are affected by the growth stage and habitat conditions. Phenology can be a key determinant of species distribution and range dynamics (Chapman et al. 2014). Phenology evolution may be a potential process during range expansion for many invasive plant species (Novy et al. 2013). Phenotypic plasticity is one of the mechanisms enabling exotics species to colonize large, environmentally diverse areas (Davidson et al. 2011; Griffith et al. 2014). The high relative growth ability should be an important characteristic of invasive plant species (Baker 1974). Fast growth results in the rapid occupation of a large space, advantageous in competitive situations (Grime and Hunt 1975). Invasive African grasses have higher relative growth rates than native, and noninvasive grasses (Baruch et al. 1989). The fast grower species may have a more opportunistic approach to pulses in resources and translates into more growth or regeneration (Miao and Bazzaz 1990). Relative growth rate (RGR) is a significant determinant of the competitive ability of exotic plant species after disturbance (Sattin and Sartorato 1997). High RGR associated with opportunistic resource acquisition (high specific leaf areas) and increased root allocation to survive summer drought may be critical for the success of plant invaders in regions with Mediterranean climates (Grotkopp and Rejmanek 2007). Phenotypic plasticity in growth may contribute to the invasion success of *Erigeron canadensis* (Mojzes et al. 2020).

Characterization of the community's vegetation in invaded and non-invaded sites and seasons

The community's characteristics of species relative abundance and diversity metrics between the invaded vs non-invaded communities are crucial to determine the importance of *S. elaeagnifolium* invasive species. Whereas, these communities are not only affected by invasion but also by many factors including the soil type, climate conditions and the used agricultural management systems. Therefore, we chose the adjacent invaded and non-invaded localities whereas, only mechanical methods are used during land preparation for weed control and no herbicides are used. The composition of weeds is related to the regional climate and soil characteristics and management methods (Dale et al. 1992; Marshall et al. 2003).whereas, the distribution from place to place over time is dependent upon soil factors and the regional climatic condition (Andreasen and Skovgaard 2009). In this research, weed population characteristics were concluded according to Thomas (1985), Relative abundance (RA) is more effective in determining and comparing the abundance of each species in the different communities. The findings showed that the invasive *S. elaeagnifolium* species affected negatively the new recipient communities. Whereas, there was a lower relative abundance of species in invaded than non-invaded areas. Abundance is an important ecological quantity necessary for monitoring invasive species (Veldtman et al. 2010). Abundance and distribution in space are positively correlated (Gaston and Blackburn 2000). Nevertheless, the effect of altitude on invasive

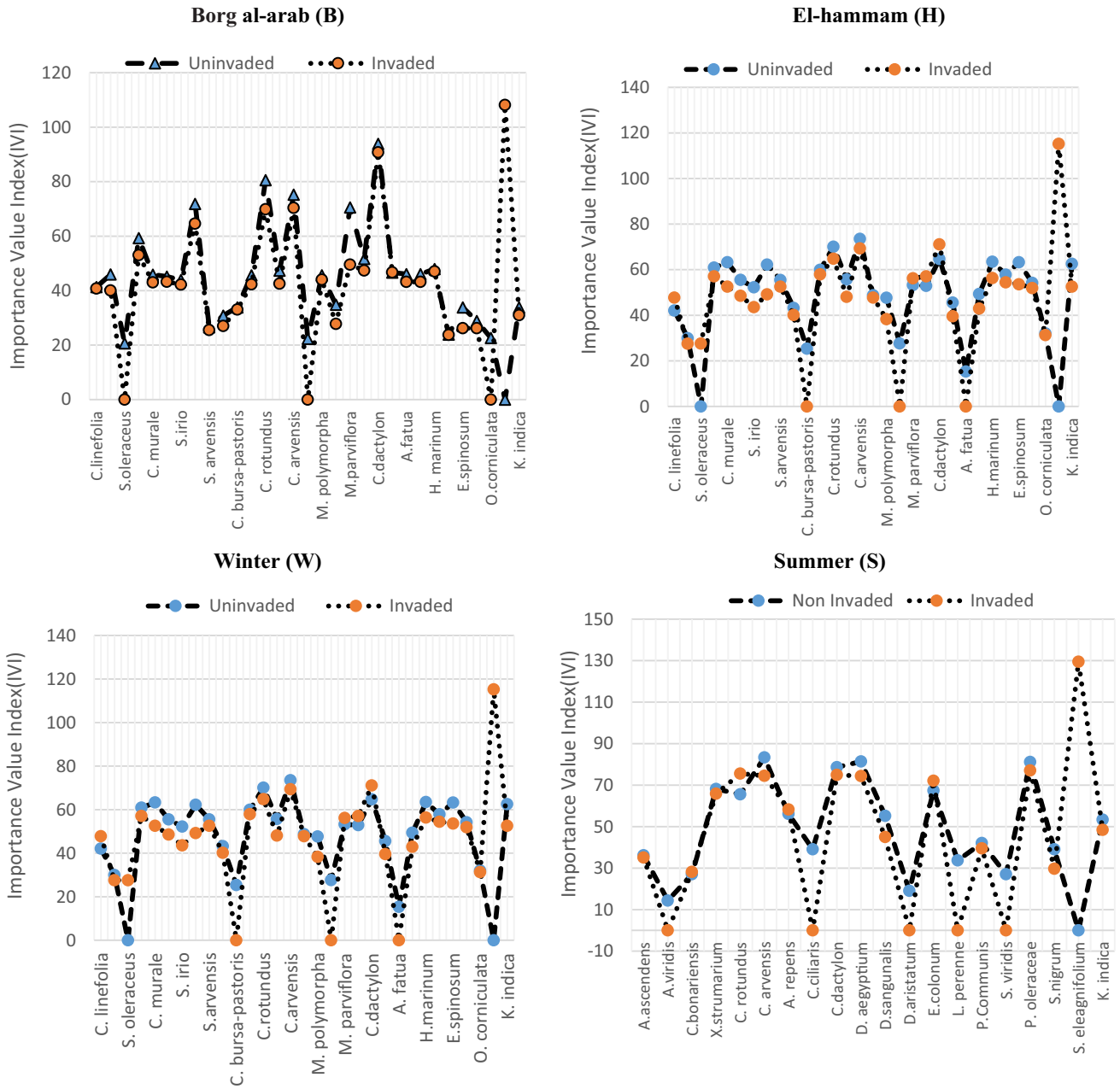


Fig. 6 Importance value index of surveyed weeds in different areas and seasons

weed distribution was more important than other environmental factors (Hassannejad and Ghafarbi 2014). The differences in the structure and composition of native community population dynamics appeared from the lower weed diversity and richness as well as evenness indexes in the invaded sites as compared with the non-invaded community, especially in the summer season. According to the results, there were some ecological indices are suitable to assess the impact of *S. elaeagnifolium* invasions such as the diversity index of Simpson index1 (λ), Shannon index (H'), Hill's index (E4) and Modified hill's ratio (E5) and Coefficient of similarity (CS) due to their high sensitivity. However, the evenness parameters of Pielou's index (E1), Shannons's index (E2), Heip's index (E3) were not appropriate due to their lowest response and sensitivity (Table 3). Additionally invaded communities have high similarity based on the coefficient of similarity as compared with uninvaded communities. The relative importance value was used to describe the impacts of invasive species on a community (Bradford et al. 2006). Invasive plants primarily had negative effects on plant diversity when

they became abundant at a much lower cover level (less than 35%), compared with the native plants (over 60%) (Qi et al. 2014). Species richness, diversity and evenness were found to be significantly reduced as the density of invasive parthenium weed increased (Nguyen et al. 2017). Lantana invasion greatly reduces the density and diversity of the vegetation in the invaded area (Singh et al. 2014). Evenness influences the level of invasion that the introduced species can promote functionality under stress (De Roy et al. 2013). Invasive species reduced local species richness (Crystal-Ornelas and Lockwood 2020). The impact of invasive plant species on resident species, communities and ecosystems is reducing species richness and abundance of native biota and decreasing their local species diversity (Olden and Poff 2003; Sax and Gaines 2003). Invasive alien species break down biogeographic realms and affect native species richness and abundance (Pyšek et al. 2020).

We can conclude that *S. elaeagnifolium* has a wide range of typical germinability in the spring and summer. It has five life developmental stages with short seedling and juvenile stages which are proper for herbicide application and control purposes, an extended flowering period (May to November) and fruiting period (April to November) and finally dispersion time in the winter season (December to February). The specific growth traits of *S. elaeagnifolium* might be important for surviving in water-limited environments. Based on growth analysis, the ascending order of crop competition was Egyptian clover > wheat > grape > maize > broad bean > fig > sesame with *S. elaeagnifolium.* Whereas, *S. elaeagnifolium* growth traits were influenced by habitats and conditions. This strong and rapid growth, as well as the highest plasticity, may have been facilitated their establishment by increasing the influence upon the recipient community characteristics and their distribution, which expected to expand in several directions in the future. These results are supported by Formozis et al. (2021), who found that the different microclimatic conditions (i.e., wind speed and air temperature, humidity, light conditions, soil moisture, and levels of photosynthetically active radiation, the height of vegetation) affect *S. eleagnifolium* invasion. The vegetation analysis exhibited the effects of invasive *S. elaeagnifolium* on species diversity and evenness in invaded vs. non-invaded resident communities. A lower value in diversity metrics and higher similarity were associated with species invasion. Finally, the specific growth traits, worthy plasticity, and abilities to impact the recipient communities might be important keys for their successful spreading in massive ranges. It is noteworthy to use this information in the prediction of its spreading and *S. elaeagnifolium* impacts in the future. This overview can minimize social and economic disadvantages, raising awareness and understanding the invasion behavior of invasive alien species to preserve the balance in the agroecosystem.

Author contribution Dr Mohamed Balah participate in all experiments of the manuscripts from germination of *Solanum elaeagnifolium*, phenological development and growth traits in different crops, as well as its effects on species diversity and evenness in invaded vs. non-invaded resident communities. Dr Whaby Hassany help in the demographic surveys in invaded vs. non-invaded communities and conducted the statistical analysis of this manuscript.

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Declarations

Conflicts of interest On behalf of all authors, I declare that there is no any conflicts of interest about this research paper.

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