Macromorphological variation of the invasive Silverleaf nightshade (*Solanum elaeagnifolium* Cav.) and its relation to climate and altitude in Morocco

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Abstract

The relationship between some morphological traits and the invasive potential of invasive alien plants has been reported. Also, biological invasion is often associated with rapid evolution in introduced species. The study aim was to provide the structure of morphological variation of the invasive *Solanum elaeagnifolium* and to assess if the invasion of Morocco was followed by a rapid evolution that may affect its invasive potential. A total of 709 individuals from 218 sites, sampled across different ecological conditions, were characterized for 12 variables. The structure of the morphological variation by Hierarchical Cluster Analysis and Linear Discriminant Analysis has determined four morphotypes. Traits related to the total number of shoots and berries are those that discriminate the most between morphotypes. The description of the four morphotypes implied a rapid evolution in this species in Morocco. This evolution has resulted in large plants with a very high number of berries. However, the smallest morphotype is still predominating and is the most invasive. The geographical distribution of the four morphotypes indicates that *S. elaeagnifolium* tended to be an R-strategist plant, especially in the most severe ecological conditions. This strategy allows *S. elaeagnifolium* to allocate most of the energy to reproduction and therefore become more invasive.

Keywords: *Solanum elaeagnifolium*, morphology traits, invasive potential, morphotypes, ecological factors.

Variabilité macromorphologique de la morelle jaune (*Solanum elaeagnifolium* Cav.) et sa relation avec le climat et l'altitude au Maroc

Résumé

La relation entre certains traits morphologiques et le potentiel invasif des plantes exotiques envahissantes a été signalée. En plus, l'invasion biologique est souvent associée à une évolution rapide des espèces introduites. L'objectif de cette étude a été d'établir la structure de la variabilité morphologique de *Solanum elaeagnifolium* et de vérifier si l'invasion au Maroc a été suivie par une évolution rapide qui pourrait affecter son potentiel invasif. Au total, 709 individus issus de 218 sites présentant différentes conditions écologiques ont été caractérisés pour 12 variables. L'Analyse Ascendante Hiérarchique et l'Analyse Discriminante Linéaire, ont pu établir quatre morphotypes. Les traits liés au nombre total de branches et de baies sont ceux qui discriminent le plus entre les morphotypes. La description des quatre morphotypes implique une évolution rapide de cette espèce au Maroc. Cette évolution a donné naissance à de grands plants avec un nombre de baies très élevé. Cependant, les plants de taille réduite prédominent et sont les plus invasifs. La répartition géographique des quatre morphotypes indique que *S. elaeagnifolium* est une plante R-stratégiste, particulièrement dans les conditions écologiques les plus sévères. Cette stratégie lui permet d'allouer la grande partie de son énergie à la reproduction et de devenir plus invasive par conséquent.

Mots-clés: *Solanum elaeagnifolium*, traits morphologiques, potentiel invasif, morphotypes, facteurs écologiques.

INTRODUCTION

Phenotypic plasticity and genetic variability are among the factors that promote biological invasion (Lee, 2002; Sexton *et al.*, 2002; Clements *et al.*, 2004; Zhu *et al.*, 2017). Species with wide distribution ranges such as alien invasive plants show local adaptations or an increased phenotypic plasticity, leading to different morphological and physiological characters in response to environmental conditions (Davidson *et al.*, 2011). This category of plants offers therefore the opportunity to explore ecological factors acting on their phenotypic expression. In their review, Davidson *et al.* (2011) evidenced that alien invasive plants were nearly always more plastic in their response to greater resource availability than non-invasive species, but this plasticity was only sometimes associated with fitness benefit. Abiotic variables such as water stress, mineral nutrient deficiency, and geographical position may have an effect in the overall plant morphology. For example, latitude is negatively correlated with plant height (Moles *et al.*, 2009), while altitude may have a significant effect in leaf morphology and plant height (Ran *et al.*, 2013). Another abiotic factor that greatly limits plant growth and development is water availability. Drought reduces plant growth by affecting several biochemical and physiological processes (Holmgren *et al.*, 2012). Morphological variability in alien invasive plants may also result from rapid evolution that follows the invasion process (Müller-Schärer *et al.*, 2004; Whitney and Gabler, 2008). Furthermore, it has been reported that the use of chemical control techniques on alien invasive plants can be affected by the wide variation in some morphological traits (Zhu *et al.*, 2013a).

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First described in 1795 by Cavanilles, *Solanum elaeagnifolium* (Solanaceae) is a deep-rooted summer-growing perennial plant native to the Americas (Southwestern United States and Northern Mexico) (Boyd *et al*., 1984). It has been declared as noxious weed in its native range (Green et *al*., 1987), and one of the most alien invasive plants outside this range (EPPO, 2007; Uludag *et al*., 2016). *S. elaeagnifolium* is widely spread in Mediterranean region, Australia and South Africa (Olckers and Zimmermann, 1991; Taleb and Bouhache, 2006; Mekki, 2007; Feuerherdt, 2009). Besides Greece, Morocco is considered one of the early and highly infested country in the Mediterranean basin (Uludag *et al*., 2016). This invasive plant was first recorded in Morocco in 1944 (Gattefossé, 1952). Currently, the invasion is spreading over four climatic zones (Saharan, arid, semi-arid, and sub humid), nine soil types (gleysols, luvisols, cambisols, rankers, vertisols, complex, rendzinas, regosols, and xerosols), altitudes between 0 and 1466 m, and a wide variety of habitats: cultivated fields, roadsides, urban areas and others (Ben-Ghabrit *et al*., 2016).

Evidence exists for morphological variation of this species in the native and invaded ranges (Economidou and Yiannitsaros,1975; Boyd *et al*., 1984; Tanji *et al*., 1984; EPPO, 2007; Stanton & al, 2009; Fawzi and Habeeb, 2016; Knapp *et al*, 2017; Adjim and Kazi Tani, 2018). Despite its extensive current spread worldwide, little attention has been paid to morphological variation patterns. To our knowledge, only two studies have examined the morphological variation of *S. elaeagnifolium*. The first was conducted in Tadla region in central Morocco (Khanas, 1996). A total of 40 characters were scored for 400 plants of *S. elaeagnifolium*. Factor analysis showed that 26 of the 40 characters studied explained the most the morphological variation. The same analysis grouped the 400 individuals into 3 groups. The plants of each group differ essentially from others by the size of their organs, and no correlation between this morphological variation and geographical distribution was found. The second study was conducted on a large-scale in Australia (Zhu *et al*., 2013a). From 92 different sites, 642 plants were sampled, and 10 characters were scored for each plant. Unlike what was found by Khanas in 1996, no structure of the morphological variation was detected in Australia. However, a possible correlation between precipitation rate and morphological variability has been reported (Zhu *et al*., 2013a).

In this study, the macromorphological variation of the *S. elaeagnifolium* populations in Morocco is documented on a large-scale for the first time. In particular we focused on characters that are known to be correlated with growth rate, nutrient use and competitive ability. The study is based upon observations in the field, in sites spanning the ecological diversity in Morocco. We examined which characters are most variable and contribute to the clustering of individuals. We searched for significant relations of measured morphological characters of *S. elaeagnifolium* with abiotic variables such as altitude and water availability related to climatic zones. We also verified if there was a rapid evolution that could be related to the invasive potential. We hypothesized that the environmental pressure operating at each climatic or altitudinal type will have a significant effect in the overall morphology of *S. elaeagnifolium*. More specifically, we expect that *S. elaeagnifolium* individuals growing at drier, warmer, and higher altitudinal sites (i.e. arid and mountainous zones) will exhibit reduced height and shorter reproductive and vegetative structures compared to individuals growing at water and more temperate sites.

MATERIALS AND METHODS

Collection sites

To measure the macromorphological variation of *S. elaeagnifoilum* in Morocco, we extensively prospected the country in 2015 to find as many diverse sites as possible (Figure 1). We selected 218 sites across four climatic zones (Saharan climate, arid climate, semi-arid climate and sub humid climate), and four altitude ranges (below 300 m, from 300 to < 500 m, from 500 tow 1000 m, and above 1000 m). All characteristics of these sites were detailed previously by Ben-Ghabrit *et al*. (2016). A site consisted of one or more foci of *S. elaeagnifolium* spaced by no more than 100 meters from one another. Meanwhile, sites were separated by a few kilometers. A total of 709 individuals were sampled in this study from September to October, which represented the main period of the fruit set in Morocco. Within each site, one to twelve individuals, spaced by more than 20 meters, were selected pending upon the infestation level of the site. For a less infested site (less than 10 plants), only one plant was characterized. Whereas for a heavily infested site (more than 500 plants), 12 plants were characterized. In order to avoid the shade effect on morphological traits reported by Boyd and Murray (1982), we targeted only plants exposed to sunlight.

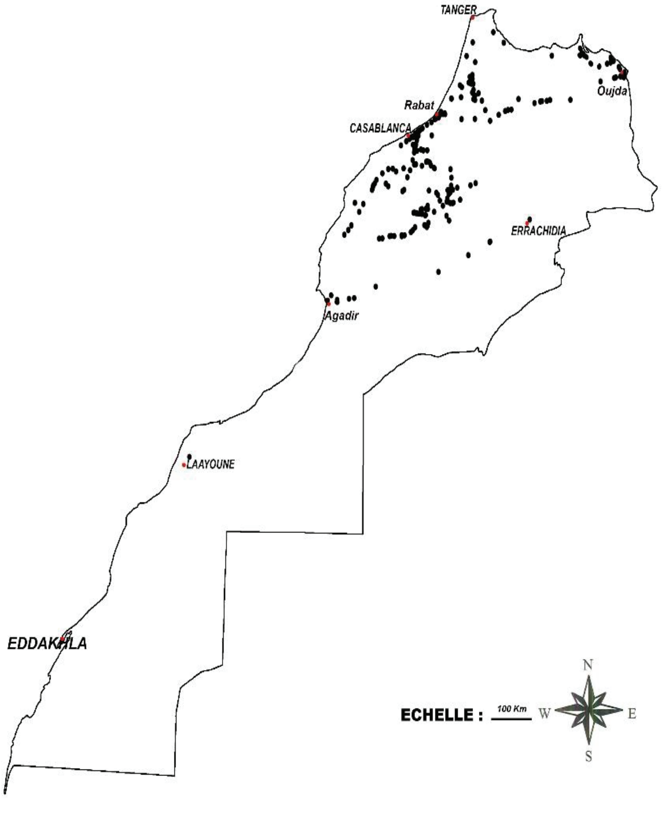

Figure 1: Map showing locations of sampling sites from the current range of Solanum elaeagnifolium in Morocco

Characters measurements

A total of 12 characters were scored for each plant in situ: **1-** plant height (measured from the ground level to the top shoot apex); **2-** stem diameter (measured at the base of the stem); **3-** total number of shoots; **4-** total number of berries; **5-** petiole length; **6-** leaf length; **7-** leaf width (the last three characters were scored for the leaf that appeared to be the largest one); **8-** the prickle density on the stem (visually assessed by using a scale from one to three: one expressed the absence or the presence of less than 10 prickles on one part of the stem; two expressed the presence of prickles with low density level (10 – 100 prickles); three expressed the presence of prickles on the entire stem with high density level (more than 100 prickles)); **9-** the total number of prickles on one petiole; **10-** the total number of prickles on one leaf; **11-** the total number of prickles on one peduncle; **12-** the total number of prickles on one calyx.

Statistical data analyses

For each character (further referred to as "variable") a descriptive analysis (mean, minimum and maximum values and coefficient of variation) was performed using XLSTAT 2018 (addinosoft, Paris, France).

Clustering analysis was performed using DARwin software version 6.0.015. First, we generated distance matrix using Manhattan distances divided by the number of variables (Perrier *et al.*, 2003):

$$d_{ij} = \frac{1}{k}\sum_{1}^{k}|x_{ik} - x_{jk}|$$

With: d_{ij} = dissimilarity between individuals *i* and *j*;
X_{ik} and X_{jk} = k variable values for individuals *i* and *j*;
k = number of variables.

Then we applied two different hierarchical clustering methods i.e. the UPGMA "Unweighted Pair Group Method with Arithmetic mean" (Sokal and Michener, 1958) and the Ward method (Ward, 1963). Though UPGMA is the most applied algorithm in Hierarchical Clustering Analysis (HCA) (Peeters and Martinelli, 1989; Odong et *al*., 2011), the Ward method also widely applied, tends to be considered as more efficient in terms of cluster detection, by minimizing the total within-cluster variance (Odong *et al*., 2011). For each method, we calculated the CPCC "Cophenetic Correlation Coefficient" (Odong *et al*., 2011) to evaluate the accuracy of the dendrograms obtained. Odong *et al*. (2011) have set a limit for the difference between the two CPCC values of the two methods. If both methods have a CPCC value higher than 0.8, Ward method will be preferred; if only UPGMA has a CPCC value higher than 0.8, and difference between UPGMA and Ward values is more than 0.1, UPGMA well be preferred. If the difference is less than 0.1 between the two CPCC values, both methods are retained.

To further evaluate the accuracy of the Ward clustering analysis we also conducted a Linear Discriminant Analysis "LDA" as suggested by Ben-Ghabrit *et al*. (2019). By performing regression analyses, LDA predicts the distribution of individuals in the clusters established by Ward and quantifies the contribution of each variable to each cluster. The overall accuracy percentage of distribution can be used as another indicator of the accuracy of Ward clustering. LDA was conducted using PAST 3 software (Ben-Ghabrit *et al.*, 2019).

The assumption of equal variances was verified using Bartlett test. As the assumption was violated and the number of individuals per group was not equal, a one-way ANOVA with Welch's F-test (Welch, 1947) using the post hoc test Games-Howell for multiple comparisons of unequal variances was performed at a significance level of α = 0.05 using XLSTAT 2018.

Finally, to illustrate the possible effect of the climate and the altitude on the occurrence of the four morphotypic groups, frequency of distribution of each group was calculated using XLSTAT 2018. The four classes of climates and of altitudes considered in the present study were described in the collection sites section.

Table 1: Mean values ± standard deviation, minimum, maximum and coefficients of variation (CV) of 12 characters (variables) of *Solanum elaeagnifolium*

Characters (Variables)	Mean ± SD	CV (%)	Min	Max
Plant height (cm)	62.3 ± 20.5	32.9	14.0	130.0
Stem diameter (mm)	8.7 ± 3.4	39.6	1.1	27.9
Total number of shoots per plant	14.2 ± 13.6	96.2	1.0	175.0
Leaf length (cm)	6.7 ± 2.4	36.0	1.8	17.2
Leaf width (cm)	1.8 ± 0.8	45.4	0.4	6.9
Petiole length (cm)	1.4 ± 0.9	63.0	0.2	7.1
Total number of berries per plant	70.6 ± 116.3	164.6	0.0	1841.0
Prickle density per stem	1.7 ± 0.8	46.0	1.0	3.0
Total number of prickles per leaf	0.8 ± 2.6	315.1	0.0	21.0
Total number of prickles per petiole	0.9 ± 2.5	266.1	0.0	22.0
Total number of prickles per peduncle	3.6 ± 4.7	128.7	0.0	32.0
Total number of prickles per calyx	4.3 ± 5.6	130.9	0.0	25.0

RESULTS

Level of morphological variation

A total of 709 plants were characterized *in situ*. *Solanum elaeagnifolium* is morphologically diverse in Morocco as all characters had large ranges (Figure 2) and high coefficients of variation "CV" (Table 1). Four characters related to prickles (corresponding to the total number of prickles per leaf, petiole, peduncle and calyx) showed values of CV higher than 100 %. The total number of prickles per leaf showed the largest variation (CV of 315.1 %). These four characters ranged from 0 to 21 -35 total numbers which corresponds to a 21-fold to 35-fold increase. The total number of shoots and berries per plant also showed a large variation with CV of 96.2 % and 164.6 %, respectively. The mean value of the total number of shoots and berries was 14.2 and 70.6 respectively. We found six individuals which bore more than 500 berries, and even one individual with 1841 berries and 175 shoots (Figure 3).

Although CV values of plant height and leaf length were 32.9 % and 36 % respectively, plant height varied from 14 to 130 cm and leaf length varied from 1.8 to 17.2 cm, meaning that the tallest plant and the longest leaf were 9 times larger than the shortest plant and leaf. Both variables stem diameter and petiole length had CV values of 39.6 % and 63 % respectively, however the stem diameter varied from 1.1 to 27.9 mm and the petiole length varied from 0.2 to 7.1 cm, which indicates a large morphological variation (Table 1).

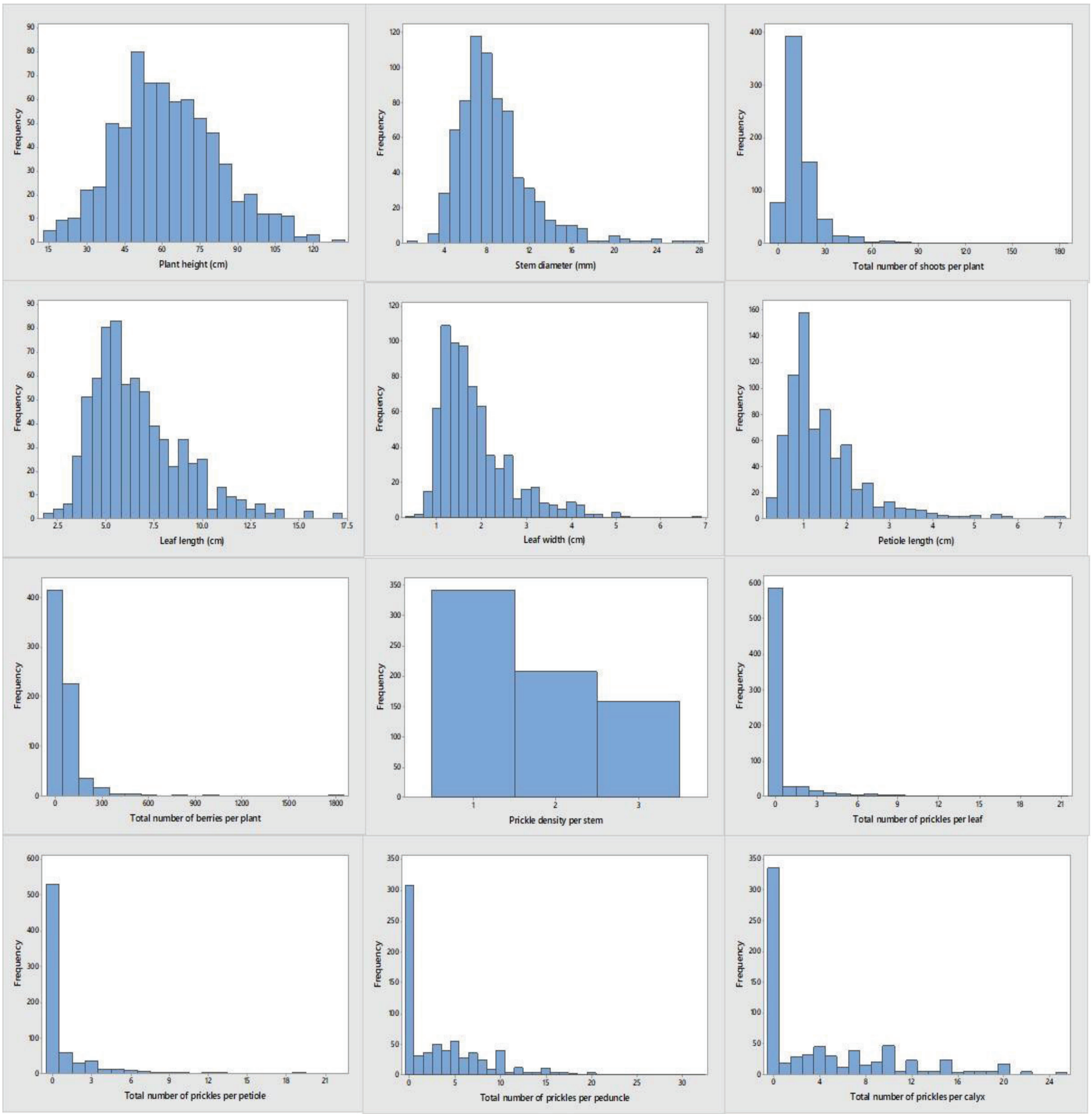

Figure 2: Frequency distributions of the morphological characters of Solanum elaeagnifolium

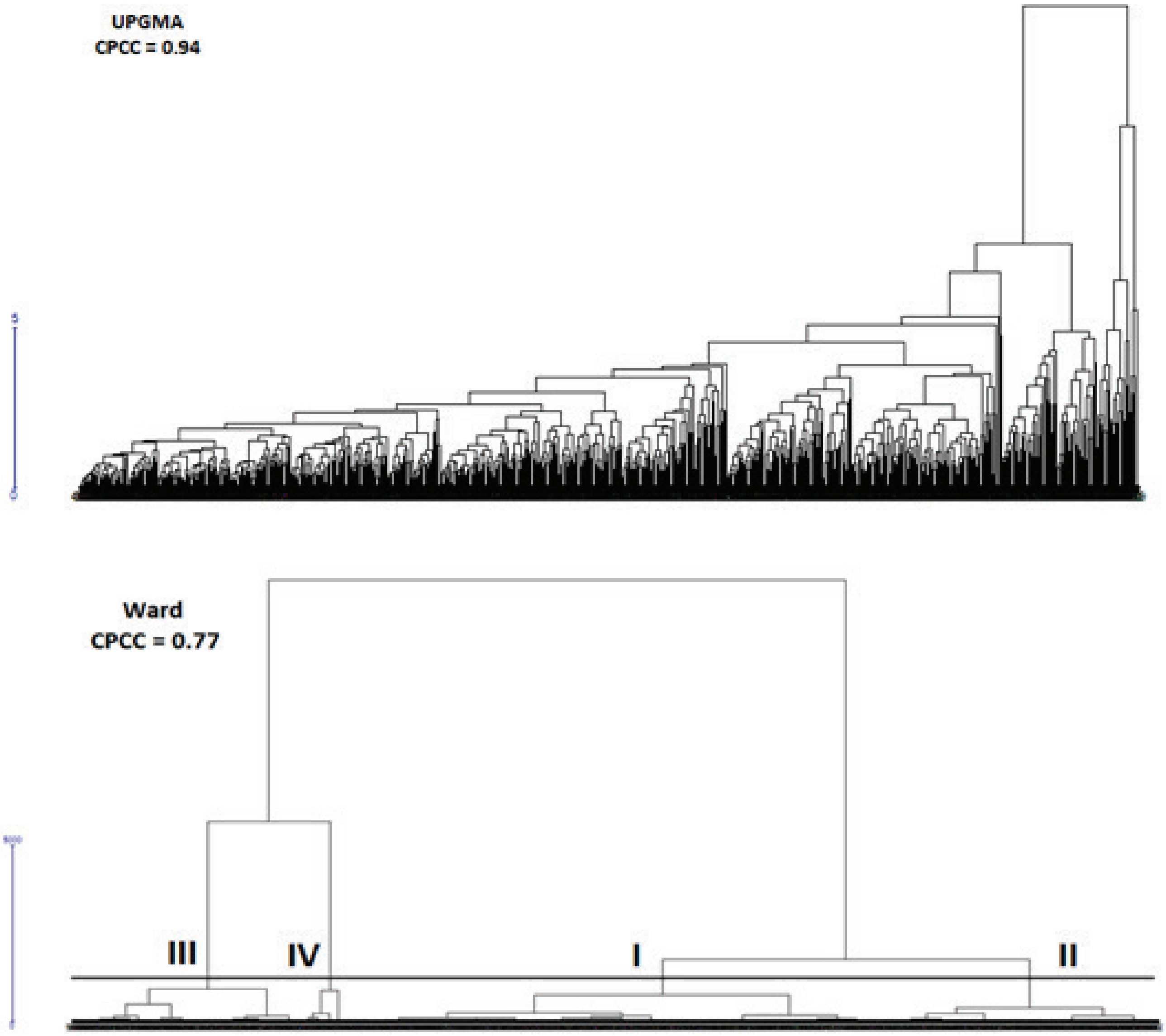

Figure 4: Clustering analysis of S. elaeagnifolium by UPGMA (above) and Ward (below) and their corresponding Cophenetic Correlation Coefficient (CPCC)

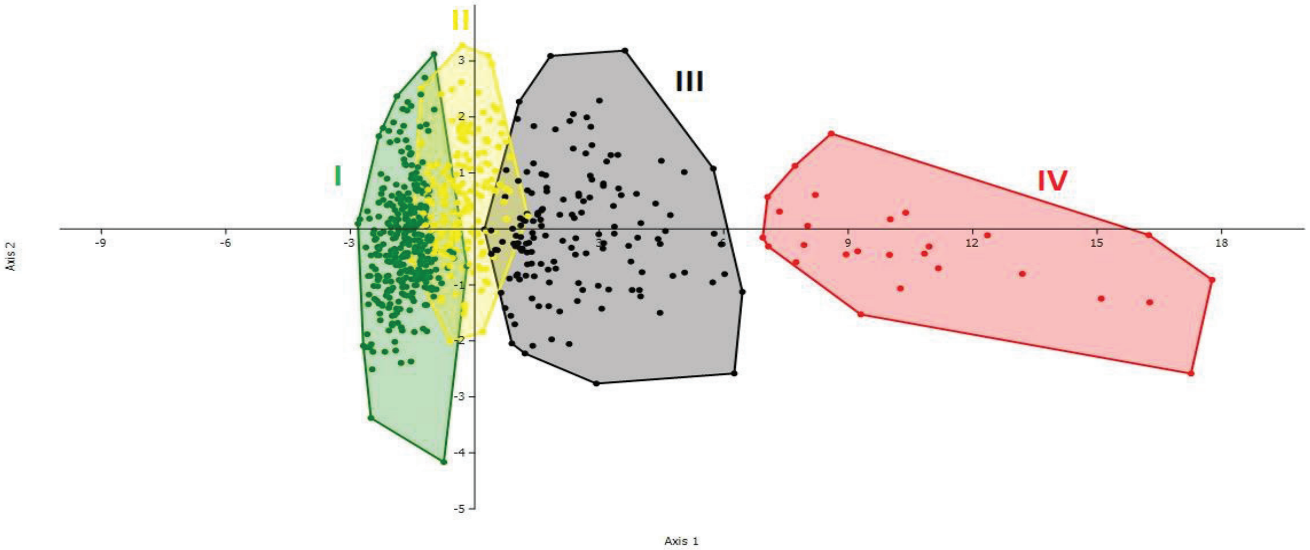

Figure 5: Distribution of S. elaeagnifolium across the four clusters by linear discriminant analysis (LDA)

Figure 3: A Solanum elaeagnifolium plant with 1841 berries and 175 Shoots

Morphotypic groups

In order to maintain the accuracy of the cluster analyses, we excluded from the data set the six individuals with the highest values of branches and berries number. Unlike the UPGMA that could not distribute the remaining 703 individuals into well-defined clusters, Ward's method clustered them into four distinct clusters (morphotypes) (Figure 4).

The CPCC values of the two dendrograms had a difference of 0.17. This indicates that according to the limit set by Odong *et al*. (2011) the probability that these four clusters are artefactual is no longer negligible. The LDA predicted the distribution of individuals among the four morphotypes with an overall accuracy of 88 % (Table 2). morphotype IV was clearly distinct from the other morphotypes. morphotypes I and III were well separated from each other, while morphotype II was only an intermediary cluster between I and III morphotypes (Figure 5). Table 2 and figure 5 showed that the loss of accuracy is mainly due to the fact that morphotype II is only an intermediary group between morphotypes I and III, which led to a misclassification of individuals between morphotype II on one side and morphotypes I and III on the other side. Therefore, the results of the LDA indicate the validity of Ward's discrimination despite the difference between the two values of CPCC.

Table 2: Classification of *S. elaeagnifolium* plants in four clusters by linear discriminant analysis (LDA)

		Observed clusters			
		I	**II**	**III**	**IV**
Predicted clusters	**I**	305	30	0	0
	II	36	157	17	0
	III	0	1	129	0
	IV	0	0	1	27
Accuracy percentage (%)		89	84	88	100
Overall accuracy percentage (%)		88			

Given that the contribution of axis one to discrimination between clusters was 97.8 %, the total number of berries per plant was the most discriminatory variable between morphotypes, plant height and the total shoots number per plant came in second, while the other variables had a low contribution (Table 3).

Results of the Post-hoc multiple pairwise comparisons were presented in Table 4. The analyses showed that only the total number of shoots and the total number of berries per plant are significantly different between clusters, and that their mean values increased from morphotypes I to IV. In other words, individuals belonging to cluster IV are

Table 4: Grouping Information Using the Games-Howell Method and 95% Confidence

	Cluster 1		Cluster 2		Cluster 3		Cluster 4	
	Mean	**Group**	**Mean**	**Group**	**Mean**	**Group**	**Mean**	**Group**
Plant height	54.6	C	69.6	B	66.2	B	82.3	A
Stem diameter	7.3	C	9.2	B	10.2	A	12.6	A
Total number of shoots	8.7	D	12.3	C	21.9	B	38.2	A
Leaf length	6.6	A	7.0	A	6.6	A	6.1	A
Leaf width	1.8	A	1.9	A	1.8	A	1.7	A
Petiole length	1.5	A	1.5	A	1.3	A	1.1	A
Total number of berries per plant	19.4	D	53.5	C	124.4	B	343.1	A
Total number of prickles per leaf	1.0	A	0.5	B	0.9	AB	0.4	AB
Total number of prickles per petiole	1.1	A	0.6	B	1.0	AB	0.5	AB
Total number of prickles per peduncle	3.0	B	3.6	AB	5.0	A	3.4	AB
Total number of prickles per calyx	3.6	B	4.6	AB	5.5	A	3.5	AB
Prickle density on stem	1.7	B	1.7	B	1.9	A	1.7	AB

associated with phenotypes of highest number of shoots and berries. Plant height means were not significantly different only between II and III, and stem diameter between III and IV (Table 4). The three characters related to leaf features were not found to be discriminant.

Table 3: Contribution of each variable to the discrimination of the four clusters

Variables	Axis 1	Axis 2
Plant height	2.298	15.586
Stem diameter	0.504	1.667
Total number of shoots	2.652	0.173
Leaf length	-0.032	0.504
Leaf width	-0.008	0.120
Petiole length	-0.029	0.065
Total number of berries per plant	26.317	-2.371
Total number of prickles per leaf	-0.030	-0.620
Total number of prickles per petiole	-0.037	-0.589
Total number of prickles per peduncle	0.153	0.490
Total number of prickles per calyx	0.115	1.227
Prickle density on stem	0.013	-0.060

Climate, altitude and distribution of the four phenotypic groups

The analysis of the frequency of distribution of the four phenotypic groups evidenced that all groups are distributed across the four classes of altitude and of climates, except the phenotypic group IV which was not observed under the Saharan and arid climates and in site located at an altitude of more than 1000 m.

I and II predominated under the Saharan, arid and semi-arid climates. Under the sub-humid climate, we observed a predominance of the morphotype III (50 % of individuals) (Figure 6).

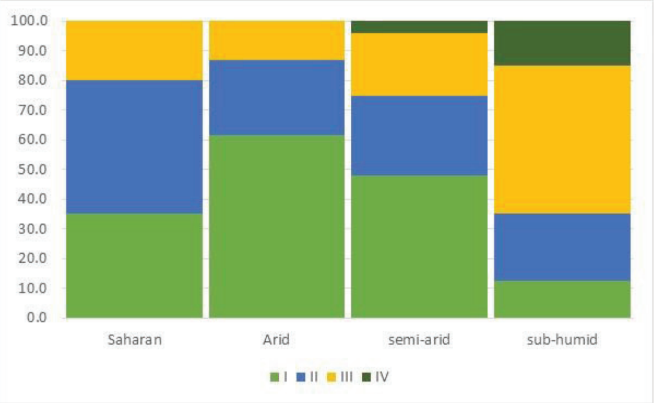

Figure 6: Distribution percentage of the four phenotypic groups according to the four climatic classes evidenced in Morocco

Below 300 m the morphotype IV had about 8 % of individuals, while between 300 and 1000 m it had only a poor appearance (1 % of individuals) and it was totally absent above 1000 m. Otherwise, morphotype I predominated in all altitude classes (Figure 7).

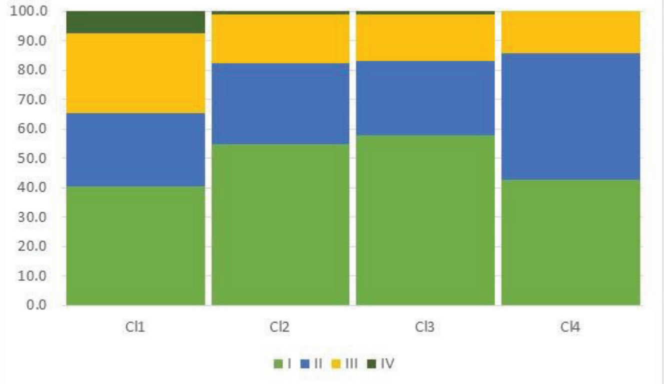

Figure 7: Distribution percentage of the four phenotypic groups according to the four altitude classes (Cl 1: below 300 m; Cl 2: 300 to 500 m; Cl 3: 500 to 100 m; Cl 4: above 1000 m) evidenced in Morocco

DISCUSSION

Phenotypic plasticity and genetic variability are among the factors that promote biological invasion (Sexton *et al.*, 2002; Genton *et al.*, 2005). Both factors have been reported in *S. elaeagnifolium* (Travlos, 2013; Zhu *et al.*, 2013b). In this study, the presence of a large morphological variation among *S. elaeagnifolium* in Morocco was revealed. Yet, a clear distinction between what is attributed to phenotypic plasticity and genetic variability could not be made.

For the first time, the morphological variation of *S. elaeagnifolium* was patterned into morphotypes. Clustering analyses were successful in separating individuals into four distinct clusters which belong to one single species. Two characters (total number of shoots end berries) were particularly diagnostic in discriminating these four clusters. Thus, four morphotypes have been established and probably a fifth is in the process of being created.

For several variables (plant height, stem diameter, branches number, berries number, leaf length, leaf width and petiole length), the maximal values recorded in this study were much higher than in previous studies (Encomidou and Yannitsaros, 1975; Boyd *et al.*, 1984; Tanji *et al.*, 1984; Khanas, 1996; EPPO, 2007; Stanton *et al.*, 2009; Zhu *et al.*, 2013a; Fawzi and Habeeb, 2016; Knapp *et al.*, 2017; Adjim and Kazi Tani, 2018). In 1996, Khanas revealed the presence of three groups of *S. elaeagnifolium* in Tadla (Morocco), based on their organ dimensions. Twenty years later, this study revealed the presence of four groups and higher maximal values than scored by Khanas in 1996. This supports the rapid evolution assumption suggested by Whitney and Gabler (2008). Travlos (2013) demonstrated that plant height and seed production increase in *S. elaeagnifolium* under higher water availability. Given the fact that the six individuals having more than 500 berries were all in sub-humid areas or irrigated fields, these individuals may be simply the core of an emerging morphotype.

It was suggested that the increase in plant height and berries number indicate the increase in invasive potential of *S. elaeagnifolium* (Travlos, 2013). Mihulka *et al.* (2003), reported that the invasive potential of an alien plant is not determined by the number of seeds that it may produce. Ben-Ghabrit *et al.* (2019) showed that an excessive production of berries in *S. elaeagnifolium* in Morocco was associated with a loss of quality of produced seeds. This can be seen as a trade-off in allocation of energy resources between traits related to berry production and those related to the germination rate (Ben-Ghabrit *et al*., 2019). Ben-Ghabrit *et al*. (2019) found that the invasive potential of *S. elaeagnifolium* increases in the most severe ecological conditions. Giving the fact that the smallest morphotype (I) was found to be predominated in those ecological conditions, this implies that the small-sized individuals are the most invasive for this species. All this suggests that *S. elaeagnifolium* is an R-strategist plant rather than a K-strategist one, especially in the most severe ecological conditions. The R-strategists plants are known to be small, rapidly maturing and produce more seeds with a high germination rate (Pysšek and Richardson, 2008). This strategy allows *S. elaeagnifolium* to minimize its life cycle in order to take advantage of the short rainfall season (especially in Saharian, arid and semi-arid climates and the mountainous regions) and allocate most of the energy to reproduction. Vuković *et al*., (2014) categorised *S. elaeagnifolium* as a C to SC-strategist plant according to grime's CSR model (Competitive, Stress tolerant, and Ruderal) (Grime, 1979). The description of morphotype I (small size, low branching, high reproduction) indicates that this species could also be categorized as an R-strategist plant according to the Grime model.

Many environmental factors affect the effectiveness of chemical treatment of weeds. Water availability, water quality and exposure to dust are environmental factors that have been proven to influence the effectiveness of the chemical treatment of *S. elaeagnifolium* (Bouhache *et al*., 1996). Leaf size is a morphological factor that can influence chemical treatment of weeds (Zhu *et al*., 2013a). Despite the large variation recorded in this study (the largest leaf is nine times bigger than the smallest one), no significant difference was found between the four morphotypes. This means that leaf size changes independently of other factors. Thus, no specific treatments according to the morphotype can be applied. However, there are other morphological factors that may influence the chemical treatment, such as trichome density (Zhu *et al*., 2013a), but they were not included in this study. Studying the trichome density in each of the four morphotype may provide new elements to chemical control of *S. elaeagnifolium*.

CONCLUSION

This study aimed to provide the structure of the morphological variation of *Solanum elaeagnifolium*. For the first time, plants of this species were patterned into four morphotypes. Traits related to plant size and berries number are those that discriminate the most between morphotypes. The description of the four morphotypes implies a rapid evolution in the invasive *Solanum elaeagnifolium* in Morocco. This evolution has resulted in large plants with a very high number of berries. However, the smallest morphotype still predominating and is the most invasive. The geographical distribution of the four morphotypes indicates that *S. elaeagnifolium* is an R-strategist plant, especially in the most severe ecological conditions. Despite the large variation recorded in this study, no significant difference was found between leaf sizes for the four morphotypes. Thus, no specific chemical treatment according to the morphotype can be applied.

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