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Effect of Habitat Heterogeneity on the Growth and Biochemical Components of Three Plant Species Native to the Mediterranean Coast of Egypt

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UNDERSTANDING the ecological performance of desert plants in different habitats is essential for any restoration and conservation measures. The growth and biochemical characteristics of three native plants (*Thymelea hirsuta*, (L.) Endl., *Ononis vaginalis* Vahl, and *Limoniastrum monopetalum* (L.) Boiss) were studied. The growth and biochemical parameters attained maximum values in the saline depressions and the lowest values in the coastal dunes. The growth criteria were significantly different among the habitats of the studied species except for the stem height, and the number of branches/plant for *T. hirsuta*. *T. hirsuta* and *O. vaginalis* shoots attained significantly higher macronutrient content in drier habitats than *L. monopetalum*. All the stoichiometric (concentration) ratios were significantly different among the habitats of *L. monopetalum* and *O. vaginalis* (except C/N and C/K ratios). The insignificant differences in *T. hirsuta* stoichiometric ratios indicate its tolerance to stress conditions. The significant variations in the species content of biochemical compounds reflect the gradients in habitats' edaphic resources. High species carbohydrate content in saline depressions and rocky ridges indicates more stress on these species. PCA ordination revealed that *T. hirsuta* dominates in habitats with low salinity, significantly high soil moisture, and bicarbonates. Meanwhile *O. vaginalis* prefers soil rich in bicarbonates, Fe, P, sand, and gravel content. *L. monopetalum* seems to be more influenced by the soil properties than the other species. The revealed insights on the plant-soil interactions and species distributions could help in future conservation measures and sustainable use of the species in the coastal Mediterranean arid environments.

Keywords: Biochemical parameters, Dry biomass, Indicator species, Phenotypic plasticity, Stoichiometry.

Introduction

High environmental variability among habitats of plant species affects their persistence and population dynamics (Farahat et al., 2015; Buckley & Puy, 2022). Deciphering the mechanisms of interactions among plant communities and the surrounding environmental factors is of main interest for understanding what shapes plant species composition and structure in different habitats (Lennon et al., 2011; Zhong-hua et al., 2013; Slima et al., 2021). Studying the role of environmental variables is crucial for detecting differences in the geographical distribution of plant species; and, for understanding the species' environmental needs for ecological restoration, management, and the establishment of new plantations (Toledo et al., 2012; Zabin et al., 2022).

Leaf mineral nutrients have an impact on the effectiveness of plant photosynthetic processes and the mechanisms involving the enzyme Rubisco (Stitt et al., 1991). Farahat et al. (2015) found that the heterogeneity of chemical resources at different distribution sites of *Calotropis*

procera populations was indicated by the variability of the foliar nutrients' concentration. The study also revealed that *C. procera* exhibited plastic responses in the functional traits and foliar nutrient contents in different urban habitats, which reflected the variations in soil resource gradients. Wang et al. (2022) noticed that invasive and native species demonstrated a similar trend in the effect of nutrient requirements on total biomass plasticity. Species with high nutrient demands demonstrate more total biomass plasticity in comparison to those with low nutrient needs.

Plants produce secondary metabolites in response to environmental stresses because they have a variety of protective functions (Edreva et al., 2007; Abdel-alim et al., 2023). El-Sherbeny et al. (2021) found that *Artemisia monosperma* and *Limrada crithmoides*, two species growing naturally along the Mediterranean coast of Egypt, had significant high levels of tannins, alkaloids, phenolics, flavonoids, and antioxidant activity. Abd El-Maboud & Abd Elbar (2020) detected that *L. monpetalum* along the Mediterranean coast in Egypt accumulated proline and total phenols and regulated the foliar nutrients under stress conditions besides morphological and anatomical responses. Both plant nutrient stoichiometry and resorption efficiency are regarded as crucial functional characteristics, and they often change as the environment does (Tong et al., 2021). According to Luo et al. (2021), most soil factors in Xinjiang, China, had a direct impact on the N and P stoichiometry in several organs of desert plants, whereas climate factors had an indirect impact on the stoichiometry via modifying soil factors.

Habitat heterogeneity is a crucial landscape feature that affects patterns of biodiversity and consequently conservation measures (Tuanmu & Jetz, 2015). Although there is a strong relationship between heterogeneity and diversity of plants (Lundholm, 2009), understanding the phenotypic plasticity of certain species under different habitats is essential for helping in any related restoration or conservation program. We proposed that the more plastic responses of the species to the environment will support its distribution and vice versa. Therefore, this study aimed to investigate the phenotypic plasticity of the biochemical and growth characteristics of three plant species (*Thymelea hirsuta* (L.) Endl., *Ononis vaginalis* Vahl, and *Limoniastrum monopetalum* (L.) Boiss) that are naturally

growing in different habitats of the Mediterranean coastal region in Egypt. Additionally, the plant-soil relationships in different habitats were discussed. The studied species are Mediterranean endemics and key indicators of the main habitats of the northwestern coastal deserts of Egypt, additionally, they have been threatened by the reduction in their populations as well as the exponential loss and degradation of their natural habitats brought on by recent human activities (Halmy, 2012, 2019; Halmy et al., 2015a, b). The current study attempted to assess the differences in the species-specific response to the abiotic soil conditions in each habitat and how that reflects the phenotypic plasticityof each species. We hypothesized that the more flexible responses of the species to the environment will help in its distribution and vice-versa.

Materials and Methods

The study area

The western Mediterranean coastal region in Egypt (Fig. 1) extends for 500 km from Alexandria to Sallum and is considered the richest phytogeographical region in plant diversity in Egypt (Heneidy & Bidak, 2004). A diverse set of habitats ranging from coastal dunes (sand dunes hereafter), rocky limestone ridges, salt marshes, non-saline depressions, saline depressions, sand formations (sand plateau hereafter), and inland plateaus that stretch parallel to the coast characterizes the region. Drought, salinity, soil erosion, and anthropogenic disturbances (urban development, agriculture, and quarrying) represent major threats to the natural vegetation of the northwestern Mediterranean coast (Halmy, 2012; Ahmed et al., 2014; Ciccarelli, 2015; Halmy et al., 2015a).

Plant sampling and measurements

Three perennial plant species namely *T. hirsuta* (Family Thymelaeaceae), *O. vaginalis* (Family Fabaceae), and *L. monopetalum* (Family Plumbaginaceae) were collected from different habitats (These habitats are coastal dunes, rocky ridges, roadsides, sand plateaus, and saline depressions) in the region. *T. hirsuta* and *O. vaginalis* were collected from three different habitats while *L. monopetalum* was collected from four habitats. Each habitat was represented by 3 replicates at least. In the field, the aboveground shoots of each species were sampled from 10 quadrats (25×25cm) at their habitats. In situ,

plant maximum height was measured, while the number of branches/plants was counted in the laboratory. Plant materials were air-dried for many days until reaching constant weight, sorted into leaves and stems, then ground and powdered using an electrical grinder. The powdered samples were kept in the refrigerator at 4ºC until further chemical analysis. The mean dry weights (g) of the total aboveground parts stem, and leaves were determined for each species.

Soil sampling and analysis

Soil samples were collected from the different habitats at a depth of 0-30cm. For each sample, soil moisture was measured in the field using a soil moisture meter (PASPORT Soil Moisture - PS-2163) and as close as possible to the root system of the sampled plants. The collected soil samples were sieved with different pore-size sieves, and soil texture was calculated. Soil-water extracts 1:5, v/v) were prepared for pH and electric conductivity (EC) measurements. The pH was measured by JENWAY 3510 pH meter, conductivity was measured by (conductivity meter 60 Sensor, Operating Instruction Corning). Bicarbonates (CaHCO$_3$%) were determined by titration against 0.01N HCl (Allen, 1989). The concentrations of Fe, P, Ca, Mg, Na, and K were determined in the leaves of each sample using a Microwave Plasma Atomic Emission Spectrometer (MP-AES 4200, Agilent Inc.) at the Ecology Laboratory, Faculty of Science, Helwan University. The instrument settings were adjusted according to the manufacturer's guidelines. The concentrations of the elements are expressed as ppm (mg kg^{-1}).

Phytochemical analyses

The phytochemical analyses of the sampled plants were carried out from dry plant powder of leaves as follows:

Total soluble, insoluble, and total carbohydrates

An amount of 50mg of dry powder was used for the extraction of carbohydrates with aqueous ethanol (70%). The solutions were centrifuged at 4000 rpm for 15min and then increased to 25mL with de-ionized water. Total soluble carbohydrates (TSC, mg. g^{-1} DM) were determined by the Anthrone method (Umbriet et al., 1959), where 2mL of Anthrone reagent was added to 1mL of the plant extract and then incubated on a boiling water bath for 3min. After cooling, the developed color was measured by a spectrophotometer at 620nm. Glucose was used as a standard to correct the TSC content.
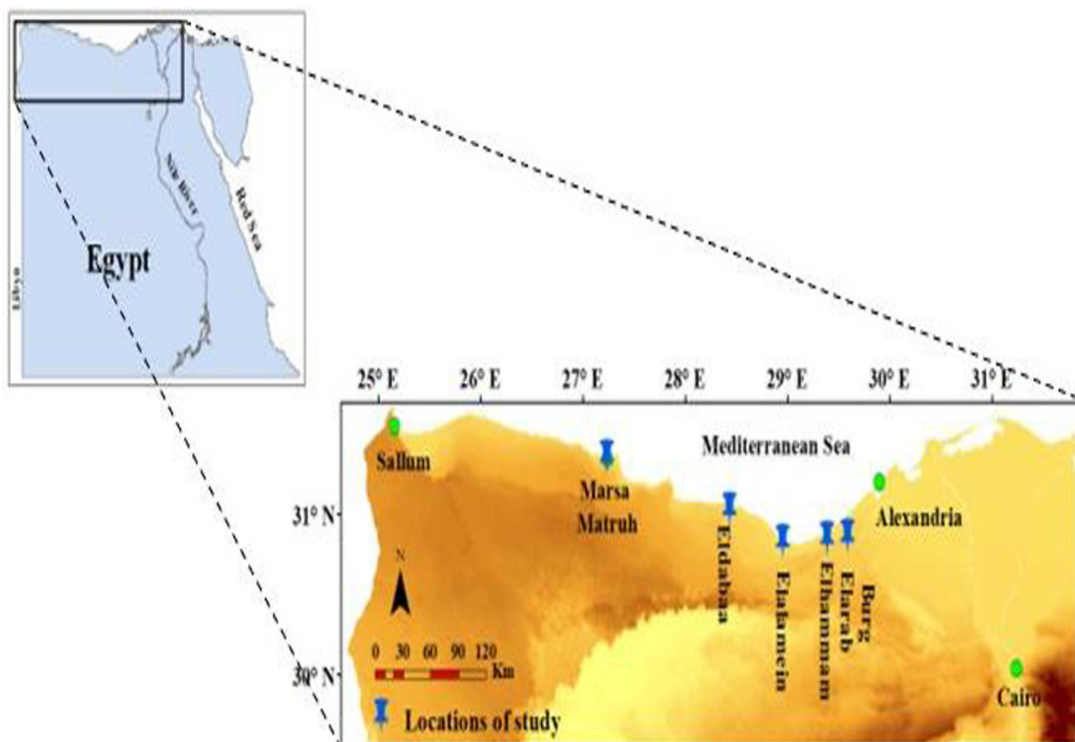

Fig.1. Map of the study area showing sites of the studied plant species along the western Mediterranean coast of Egypt.

To quantify the total carbohydrates (TC, mg g^{-1} DM) in each sample, 30mg of powdered sample was hydrolyzed in 10mL of 1 N H_2SO_4 in digestion tubes at 80°C for 8h., then the digest was made up to a definite volume. Then the total carbohydrates were calculated by the Anthrone technique. After calculating the TC and TSC, the insoluble carbohydrates were estimated according to the following equation:

Insoluble carbohydrate= Total carbohydrate – total soluble carbohydrate

Total soluble proteins

The amount of 50mg dry powder was dissolved in 10mL ethanol 70% to extract total soluble proteins. The extracts were centrifuged at 4000 rpm for 15min then the volume was increased to 25mL using de-ionized water. The total soluble proteins (TSPs) were assessed in mg. g^{-1} DM using Bovine serum albumin as a standard (Lowry et al., 1951). Plant extract (1 ml) was mixed with 5 ml of reagent C, which is made by mixing 50:1 of reagent A and reagent B respectively. Reagent A consists of 2% Na_2CO_3 in 0.10 N NaOH, while reagent B consists of 0.5 % $CuSO_4.5H_2O$ in 1% potassium tartrate. The mixture was incubated for 10min at room temperature then 0.5mL of Folin-phenol reagent (1:3) was added rapidly, mixed then completed to a definite volume. The mixture was incubated for 30min then the total soluble proteins concentration was estimated calorimetrically at 750nm by UV-Visible spectrophotometer.

Proline

Under stress conditions, proline rises proportionally faster in plants compared to other amino acids. It was assessed using the acid-ninhydrin method (Bates et al., 1973), by mixing 0.5g powdered samples with 10mL of 3% sulfosalicylic acid and filtering the mixture through a No. 1 Whatman filter paper. A mixture of 2mL of the filtrate, 2mL glacial acetic acid, and 2mL of acid-ninhydrin reagent (1.25g ninhydrin combined with 30mL glacial acetic acid, and 20mL of 6 M phosphoric acid) was incubated in the water bath at 100°C for an hour, then cooled on ice. After cooling, 4mL toluene was added, and the solution was shaken vigorously for 15-20sec using a vortex stirrer. The chromophore (red-colored upper layer) containing toluene was aspirated from the aqueous phase and left for a while at room temperature for cooling. The absorbance of the colored solution was measured at 520nm using toluene as a blank.

The concentration of proline was estimated as mg proline/g dry weight from a standard curve.

Total antioxidant capacity

The ferric-reducing antioxidant property of the plant methanolic extract was determined by mixing 1mL extract with 2.5mL of potassium buffer (0.2 M, pH 6.6), and 2.5mL of 1% potassium ferricyanide [K_3Fe (CN)6] in a volumetric flask. The mixture was vortexed well, incubated at 50ºC for 20min, and then combined with 2.5mL of 10% trichloroacetic acid and centrifuged at 4000 rpm. for 10min. The colored liquid resulting from combining 2.5mL of the supernatant, 2.5mL of DI water, and 0.5mL of 0.1% ferric chloride, was measured at 700nm against the blank concerning the standard solution using UV Spectrophotometer (Chu et al., 2000).

Total phenolic content

Total phenolic content was estimated in methanolic extract according to Kujala et al. (2000) method, using Folin–Ciocalteu's reagent and gallic acid as a standard solution. The methanolic extracts were prepared by combining 0.1g air-dried powdered sample of each species with 25mL methanol 80% at 70°C for 48h. and stirring in a shaking incubator under dark conditions. Briefly, 0.5mL of filtered extract was mixed with 2.5mL Folin-Ciocalteu's reagent diluted with ethanol (1:1), and 2mL Na_2CO_3 (7.5%), stirred well then incubated at room temperature for 15min. The absorbance was measured at 765nm by a Jenway 6405 UV-VIS spectrophotometer. The total phenolic content was calculated from a calibration curve of gallic acid standard solutions and expressed as mg gallic acid equivalent (GAE) per gram of extract (mg GAE/g dry weight of extract).

Total flavonoids

Total flavonoids were extracted as total phenolic compounds and determined in the extracts using an Aluminum chloride colorimetric assay (Piyanete et al., 2009). A mixture of 0.5mL extract was combined with 150µL of 5% sodium nitrate, set to stand for 6min, then 150µL of 10% Aluminum chloride was added to the mixture, which was left for 6min, followed by adding 200µL of 1 M sodium hydroxide, then the mixture was completed to 5mL volume with methanol and mixed well. The mixture was incubated for 15min then the absorbance was measured spectrophotometrically against a blank at 510nm. The total flavonoid content was expressed in mg of quercetin equivalents (QE) per gram extract (mg QE/g). The standard curve of quercetin

was used for the calculation of the total flavonoids.

Total alkaloids

The total alkaloids were determined using the titrimetric methods (Plummer, 1990), where 1.0g of plant material was mixed up with 4mL of n-butanol, thoroughly mixed, left overnight at room temperature, and then centrifuged at 6000 rpm. for 10min, the supernatant was made up to 20mL with n-butanol. A mixture of 10mL of the supernatant and 10mL of 0.1 (N) HCl combined in a 100mL separating funnel, shaken thoroughly for 2-3min, till the separation of two layers, the lower layer comprises the alkaloids neutralized with 0.1 (N) HCl, while the upper layer contains n-butanol. The HCl portion was collected, and 2-3 drops of methyl red were mixed with it, then the slightly reddish color solution was titrated against 0.1 (N) NaOH till reaching the neutralization point that was indicated by the color change to pale yellow. The experiment was conducted in three replicas, where the mean of the total alkaloids was assessed based on the following equivalent:

1mL of 0.1N HCl= 0.0162g alkaloids

Determination of chemical cations

Estimation of chemical cations (Na, K, Mg, Fe, P) in shoot samples of the studied species was carried out using a Microwave Plasma Atomic Emission Spectrometer (MP-AES 4200, Agilent Inc.). An amount of 0.5g of powdered dry leaves (N=3 for each species in each habitat) was placed in a pre-cleaned and constantly weighed porcelain crucible, and heated in a muffle furnace at 450°C for 3h. The crucible was cooled at room temperature in a desiccator. The carbon-free ash was moistened with 2.8% Nitric acid and left overnight, then made up to a known volume. The produced solution was filtrated and used for further chemical measurements. The analysis of C and N ratios in plant materials was carried out by standard microanalysis methods using Automatic Analyzer CHNS Elementar Vario ELIII Germany at the Microanalytical Center, Faculty of Science, Cairo University, Egypt.

Statistical analysis

One-way analysis of variance (ANOVA) was applied to assess the significance of variations in the growth parameters, and biochemical and soil variables among the studied habitats. The Pearson simple linear correlation coefficient (r) was calculated to detect the type of relationship between the estimated soil variables and the plant growth and biochemical variables. The simple linear correlation analysis was conducted using the SPSS software SPSS® 15.0 (SPSS, 2006). Principal component analysis (PCA) was carried out for soil variables as a discrimination tool for the studied species in their habitats (McCune & Mefford, 2006).

Results

Physico-chemical characteristics of soil

Results showed that the soil fractions were significantly different among the studied habitats (Table 1a). The coastal dunes had the lowest values for all soil fractions except for the coarse and medium sand (15.35%±2.7 and 78.6%±4.45, respectively) for which it attained the maximum values among all habitats. Saline depression recorded the highest values of very coarse sand (9.33%±1.4) and silt (24.22%±4.09), but the lowest for medium sand (27.27%±1.88) and clay fractions (3.15% ± 0.68). On the other hand, the maximum values of fine sand and gravel were attained by roadsides and rocky ridges, respectively (Table 1a).

Chemical analysis of soil revealed that the range of pH in different habitats was 6.78-7.43, while the range of electric conductivity (EC) was 65.33-267.0 (Table 1b). The range of soil moisture content was 2.49-7.24%. The highest bicarbonate content was attained by the coastal dunes (0.09). Saline depressions had the maximum values of pH, soil moisture, Na, K, Mg, P, and Fe. In contrast, sand dunes had the lowest values of EC, Na, K, Mg, and P. Roadsides had the lowest pH value but the highest EC value (Table 1b). All the analyzed chemical variables except pH were significantly different between the studied habitats.

Growth parameters

The total aboveground dry biomass (TAGB) of *T. hirsuta* was maximum at coastal dunes (128.4 gDM.m^{-2}) followed by a sand plateau (98.6 gDM.m^{-2}) (Fig. 2). The TAGB and leaves dry weight of *T. hirsuta* were significantly different among the habitats. The highest TAGB of *O. vaginalis* (256.1 gDM.m^{-2}) was attainted in rocky ridges, with significant differences between its habitats (p< 0.05). *L. monopetalum* had its maximum TAGB (152.8 g DM.m^{-2}) at rocky ridges followed by a sand plateau (83.9 gDM.m^{-2}). The dry biomasses of the whole plant, stem, and leaves were significantly different between the studied habitats of *L. monopetalum* (Fig. 2).

TABLE 1. Physico-chemical characteristics (mean± SD, %) of soil at different habitats of the studied species [Maximum and minimum values are in bold font. Concentrations are in ppm= mg kg^{-1}]

a) **Physical variables**

Habitat	Gravel	Very Coarse Sand	Coarse Sand	Medium Sand	Fine Sand	Silt	Clay
Sand dunes	**1.28 ± 0.73**	**0.68 ± 0.4**	**15.35 ± 2.7**	**78.6 ± 4.45**	**2.45 ± 0.36**	**1.12 ± 0.57**	**0.13 ± 0.06**
Rocky ridges	**33.23 ± 1.03**	2.43 ± 0.15	**1.51 ± 0.4**	48.28 ± 1.73	9.37 ± 1.45	4.73 ± 1.11	0.25 ± 0.1
Sandy plateau	18.47 ± 1.52	4.87 ± 0.85	3.34 ± 0.74	37.73 ± 0.63	13.93 ± 1.04	19.41 ± 5.42	1.38 ± 0.32
Roadsides	4.62 ± 1.01	3.19 ± 0.52	2.95 ± 0.3	64.16 ± 4.21	**17.74 ± 1.66**	5.73 ± 1.04	1.28 ± 0.14
Saline depressions	16.82 ± 1.62	**9.33 ± 1.47**	9.63 ± 1.38	**27.27 ± 1.88**	9.25 ± 0.61	**24.22 ± 4.09**	**3.15 ± 0.68**
F-value	106.21	16.25	16.99	25.11	25.62	10.52	12.45
Significance	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001	< 0.01	< 0.001

b) **Chemical variables**

| Habitat	pH	EC (dS/m)	Soil moisture %	Bicarbonates (%)	Fe (ppm)	Mg (ppm)	Na (ppm)	P (ppm)	K (ppm)
Sand dunes	7.19 ± 0.03	65.33 ± 1.45	3.7 ± 0.26	0.09 ± 0.01	0.24 ± 0.03	2.48 ± 0.42	8.43 ± 0.46	86.43 ± 12.67	4.82 ± 0.74
Rocky ridges	7.25 ± 0.03	119 ± 7.77	2.49 ± 0.21	0.05 ± 0.01	0.27 ± 0.07	4.39 ± 0.58	27.91 ± 4.91	89.74 ± 14.16	10.72 ± 4.35
Sandy plateau	6.99 ± 0.12	76 ± 0.58	5.48 ± 0.47	0.07 ± 0.01	0.55 ± 0.23	5.52 ± 0.35	33.43 ± 7.38	116.92 ± 57.1	20.63 ± 2.88
Roadsides	6.78 ± 0.3	267 ± 21.73	4.49 ± 0.57	0.05 ± 0	0.19 ± 0.05	9.34 ± 0.82	92.76 ± 17.2	95.75 ± 18.87	15.01 ± 0.69
Saline depressions	7.43 ± 0.1	251 ± 57.94	7.24 ± 0.82	0.09 ± 0.01	0.77 ± 0.45	37.87 ± 13.61	333.24 ± 65.08	251.53 ± 6.55	81.39 ± 41.76
F-value	2.622	12.039	12.138	13.100	4.5020	23.2390	78.2715	19.1584	10.9771
Significance	0.10	0.001	0.001	0.000	0.004	0.000	0.000	0.0000	0.000
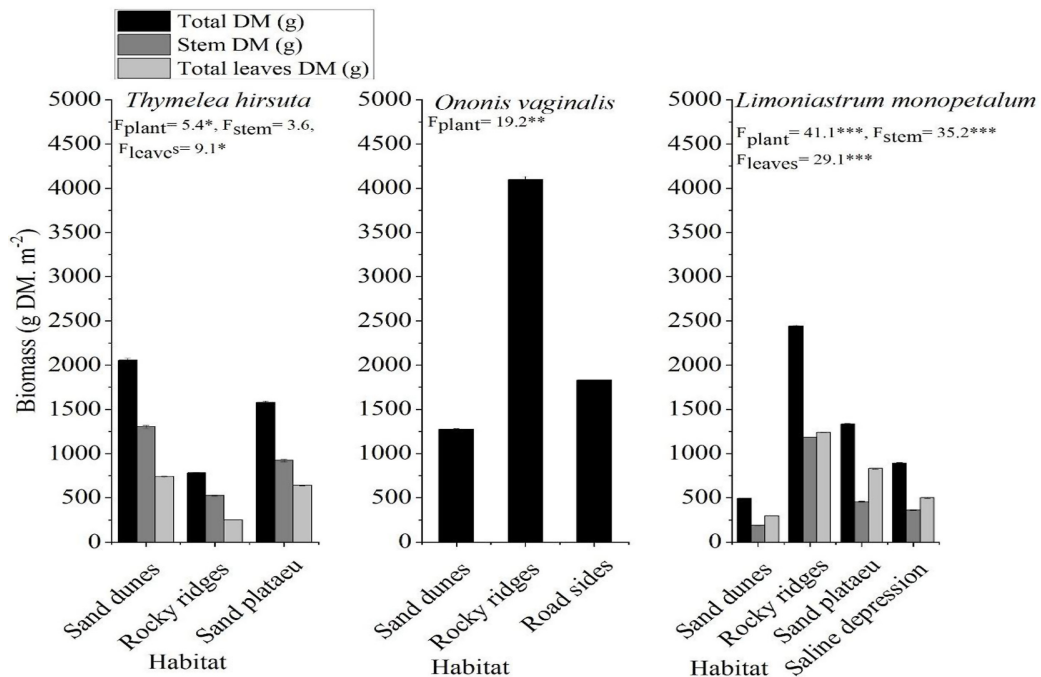
Fig. 2. Dry biomass of whole plant, stem, and leaves of the studied plant species at different habitats [Standard errors are shown on each column. F-values and asterisks showed the significance at: *** P< 0.001, ** P< 0.01, * P< 0.5]

The highest values of stem height of *T. hirsuta* (132.3cm) were recorded at the sand plateau (Fig. 3a). *O. vaginalis* had its maximum stem height at rocky ridges (35.7cm), while the lowest was at coastal dunes (22cm). *L. monopetalum* attained maximum stem height (40cm) at rocky ridges, while the lowest (22.3cm) at the sand plateau. The stem height of all species was significantly different among habitats except *T. hirsuta*. The maximum mean no. of branches per plant was attained by *T. hirsuta* (144.0) at sand dunes, *O. vaginalis* (68.7), and *L. monopetalum* (76.7) at rocky ridges (Fig. 3b). The no. of branches/ plant for *O. vaginalis* and *L. monopetalum* was significantly different between habitats at P< 0.001 and 0.05, respectively.
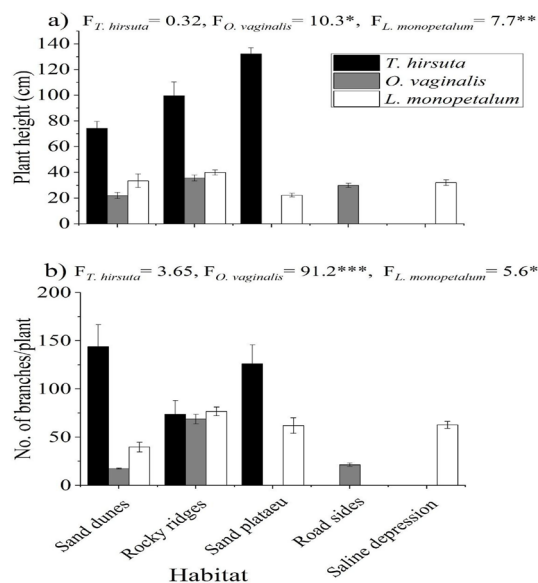

Fig. 3. Maximum stem height (cm) (a) and the number of branches (b) of the studied plant species in different habitats [Standard errors are shown on each column. F-values and asterisks showed the significance at: *** P< 0.001, ** P< 0.01, * P< 0.5]

Plant-soil relationships

The correlation analysis between the combinations of the soil physicochemical parameters and the plant biochemical parameters (Fig. 4) revealed a significant positive correlation between soil parameters and habitat types for *T. hirsuta*. EC and soil gravel fractions had a negative correlation with the dry weights of the total aboveground shoots, stems, and leaves, in addition to the no. of branches/plant. Soil pH had a significant negative correlation with flavonoids ($r = -0.83$) and phenolics ($r = -0.88$) at $P< 0.05$. Moreover, soil moisture content, very coarse sand, silt and clay content, and soil K had significant negative correlations with plant alkaloids. In contrast, silt and clay content had significant positive correlations with phenolics and flavonoids of the species. Soil moisture content and coarse sand had significant positive correlations with plant P and N concentrations, respectively.

The gravel content had significant positive

correlations with most of the analyzed parameters for *O. vaginalis* except Fe content (Fig. 4). In contrast, coarse sand and medium sand had significant negative correlations with plant height ($r = -0.84$ and -0.80, respectively), while clay content, Mg and Na had significant positive correlations with alkaloids content of the plant. Plant P was negatively correlated with soil EC, moisture content, fine sand, clay, Mg, and Na concentrations.

The plant-soil relationships for *L. monopetalum* were quite different compared to the other two species (Fig. 4). In general, the soil physical fractions and elements had a positive correlation with the analyzed plant parameters. For instance, soil pH had significant positive correlations with plant alkaloids, Mg, Na, and C (at $P< 0.05$). Soil bicarbonates had a negative correlation with the biomass of the aboveground shoots and their P content while being positively correlated with SC ($r = 0.6$) and K ($r = 0.84$).
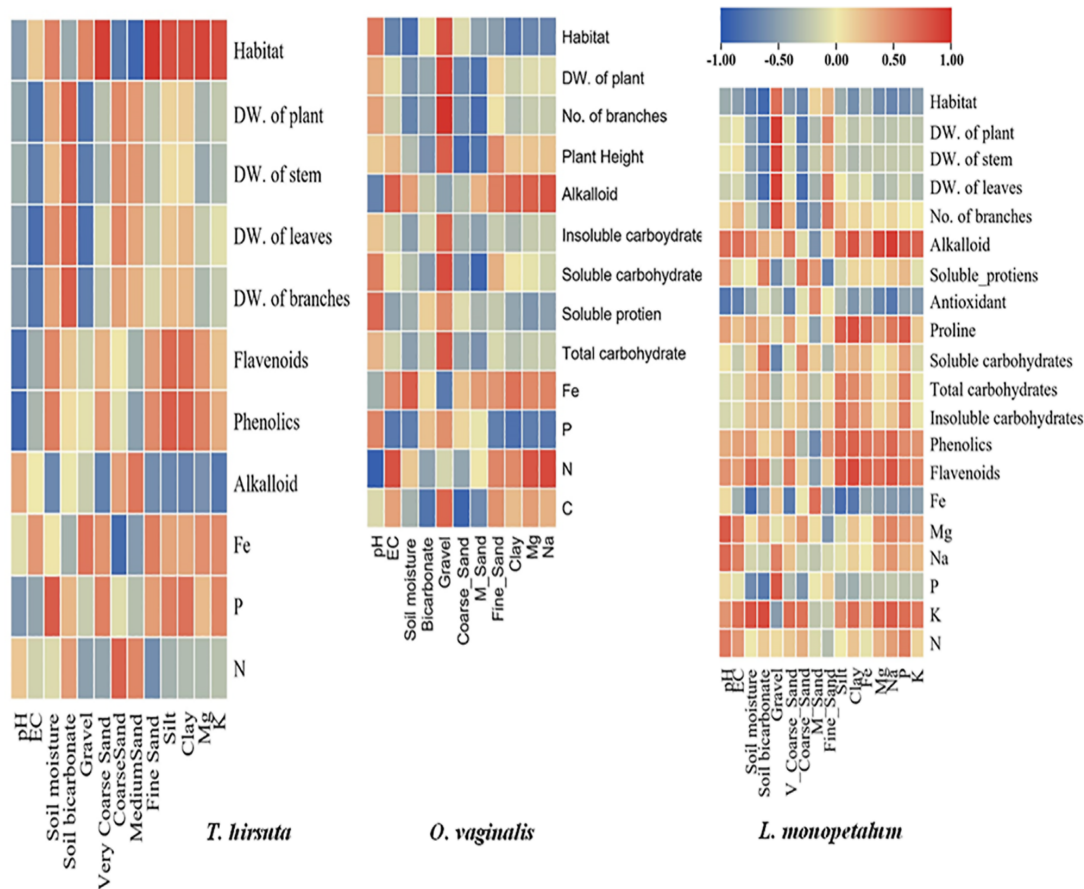

Fig. 4. Heatmap showing plant-soil relationship at the different habitats for the studied plant species

Principal component analysis (PCA)

The weights for the estimated soil variables along the first four principal components (PCs) for the studied species are shown in Table 2 and Suppl. Fig. 1a-c. The first four PCs for the target species had eigenvalues > 1. Together the first four PCs explain 93.9%, 93.7%, and 91.3% of the total variance in the habitats' properties of *T. hirsuta*, *O. vaginalis*, and *L. monopetalum*, respectively (Table 2). For *T. hirsuta*, the first PC accounted for 50.51% of the total variance and attained a high positive correlation with soil coarse and medium sand, while attaining a negative correlation with soil Mg, K, very coarse and fine sand, silt, and clay content. The second PC explained 27.15% of the total variation and attained a high positive correlation with soil moisture and bicarbonates content, while attaining a negative correlation with soil pH, EC, and gravel content. The third PC accounted for 11.67% of the total variation and showed a significant positive correlation with soil Fe while attaining a negative correlation with soil P content. In addition, the fourth PC accounted for 4.59% of the total variation and showed a weak correlation with soil K content.

For *O. vaginalis*, the first PC accounted for 50.57% of the total variance and attained a high positive correlation with soil bicarbonates and coarse sand, while attaining a negative correlation with soil minerals (Mg, K, and Na), EC, very coarse, and fine sand, and clay content (Table 2). The second PC explained 22.92% of the total variation and attained a high positive correlation with soil gravel content while attaining a negative correlation with soil moisture and medium sand content. The third PC accounted for 11.37% of the total variation and showed a high positive correlation with soil Fe while attaining a negative correlation with soil P content. In addition, the fourth PC accounted for 8.85% of the total variation and showed a weak positive correlation with soil pH and moisture content.

In the case of *L. monopetalum*, the first PC accounted for 49.93% of the total variance and attained a high positive correlation with soil medium sand, while attaining a negative correlation with most of the soil variables (Table 2). The second PC explained 22.27% of the total variation and attained a high positive correlation with soil gravel and fine sand content while attaining a negative correlation with soil coarse sand content. The third and fourth PCs accounted for 9.75% and 9.33% of the total variation, respectively, and attained weak correlations with soil factors.

Elemental analysis and stoichiometric ratios

The chemical analysis of plant leaves (Fig. 5) revealed that *T. hirsuta* had the highest value of Mg (640 ppm) and K (5915.4 ppm) at coastal dunes, Fe (586.3 ppm), and P (1146.7 ppm) at the sand plateau, while Na (2682.9 ppm) at rocky ridges. Fe and P concentrations were significantly different among the habitats at p< 0.001. On the other hand, the highest percentages of C and N were recorded at the coastal dunes (44.0% and 2.6%, respectively) (Fig. 6).

The highest values of Mg (2697.3 ppm), P (646.3 ppm), and K (4905.0 ppm) were recorded for *O. vaginalis* at rocky ridges, while Fe (814.4 ppm) and Na (2405.3 ppm) were recorded at roadsides (Fig. 5). Maximum C and N were 33.9% and 3.0%, respectively at roadsides (Fig. 6). Fe, Mg, and P were significantly different among the studied habitats of *O. vaginalis*.

L. monopetalum had the maximum values of Fe (153.6 ppm), P (559 ppm), and Na (9815 ppm) at rocky ridges habitats, while Mg (5510.0 ppm) and K (8225 ppm) at saline depressions. The highest percentages for C and N were 27.7% and 1.5% for saline depressions. Na, P, and K were significantly different among the studied habitats (Figs. 5, 6).

The stoichiometric ratios of *T. hirsuta* were higher at rocky ridges (except C: N) compared to the other habitats (Table 3). The highest values were C: P= 1420, N: P= 63.4, K: P= 16.0, C: K= 86.7, and Mg: P= 1.8. Sand plateau plants had the highest C: N ratio (26.2). There were no significant differences in the stoichiometric ratios among habitats of *T. hirsuta*. *O. vaginalis* in the coastal dunes attained the highest C: N (20.2) and C: K (77.6) ratios. In contrast, the roadside habitat had the highest values for the other estimated ratios. All the stoichiometric ratios (except C: N and C: K) were significantly different among the studied habitats of *O. vaginalis* at P< 0.01 and P< 0.001. *L. monopetalum* at coastal dunes attained the highest stoichiometric ratios of C: P, N: P, K: P, and Mg: P (16819.4, 879.4, 455.1, and 319.2, respectively) (Table 3). C: N ratio was maximum at sand plateau habitats (25.6), while C: K was maximum at rocky ridges (44.4). All the estimated stochiometric ratios for *L. monopetalum* were significantly different among the studied habitats at P< 0.05.

TABLE 2. The loadings and explained variance for soil variables in the first four PCs of the principal component analysis (PCA) [Eigenvalues for the most important variables (with absolute values higher than 0.7) in the PCA are shown in bold font]

| Species	T. hirsute				O. vaginalis				L. monopetalum			
PC	1	2	3	4	1	2	3	4	1	2	3	4
Eigenvalue	8.08	4.35	1.87	0.74	8.09	3.67	1.82	1.42	7.99	3.56	1.56	1.49
% of Variance	50.51	27.15	11.67	4.59	50.57	22.92	11.37	8.85	49.93	22.27	9.75	9.33
Cum.% of Var.	50.51	77.66	89.33	93.93	50.57	73.49	84.86	93.71	49.93	72.20	81.95	91.29
Soil variables							Eigenvectors					
Fe	-0.35	0.03	**0.86**	0.27	0.25	0.29	**0.88**	0.27	-0.39	0.14	**-0.86**	0.20
Mg	**-0.94**	-0.01	0.03	-0.13	**-0.94**	-0.29	0.07	-0.12	**-0.88**	-0.23	0.12	-0.22
Na	-0.59	-0.66	0.18	0.25	**-0.89**	-0.34	-0.13	-0.24	**-0.93**	-0.16	-0.16	-0.23
P	-0.31	0.39	**-0.85**	0.00	-0.16	0.17	**-0.80**	0.45	**-0.84**	-0.06	0.05	0.10
K	**-0.82**	0.18	0.27	**-0.45**	**-0.77**	0.01	0.50	-0.02	**-0.80**	-0.20	0.32	-0.21
pH	0.59	**-0.68**	0.25	-0.31	0.52	0.56	0.02	0.61	-0.38	-0.27	-0.60	-0.62
EC	-0.29	**-0.83**	-0.22	-0.20	**-0.94**	-0.31	0.06	-0.09	**-0.79**	-0.09	0.28	-0.43
Soil moisture%	-0.49	**0.77**	0.25	-0.23	-0.32	**-0.71**	0.18	0.54	**-0.87**	-0.18	0.24	0.24
Bicarbonates%	0.50	**0.79**	0.05	-0.02	**0.78**	-0.48	0.13	0.20	-0.50	**-0.76**	0.07	0.29
Gravels%	-0.62	**-0.75**	-0.20	-0.08	-0.10	**0.97**	0.09	-0.18	-0.07	**0.85**	0.08	-0.49
V.C. Sand%	**-0.90**	0.10	0.19	-0.27	**-0.88**	0.25	0.15	0.30	**-0.89**	0.14	0.14	-0.06
C. Sand%	**0.76**	0.51	0.02	-0.17	**0.74**	-0.50	-0.06	0.24	-0.02	**-0.91**	0.07	0.11
M. Sand%	**0.97**	0.09	0.17	-0.01	0.46	**-0.85**	0.03	-0.11	**0.79**	-0.59	-0.04	-0.07
F. Sand%	**-0.96**	-0.02	-0.04	0.20	**-0.95**	0.01	-0.17	0.19	-0.35	**0.85**	0.19	0.29
Silt%	**-0.84**	0.47	-0.11	0.18	**-0.81**	0.32	-0.11	0.20	**-0.82**	0.30	-0.13	0.45
Clay%	**-0.83**	0.53	-0.01	0.04	**-0.87**	-0.35	0.11	0.30	**-0.92**	0.05	-0.30	0.20
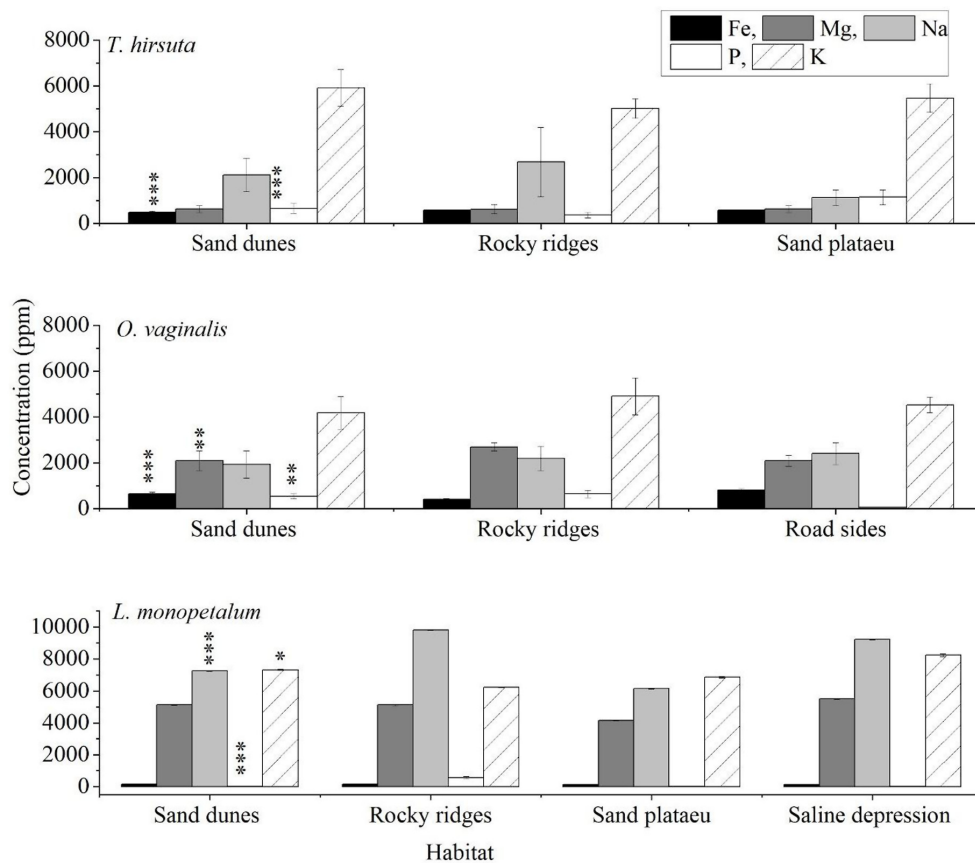
Fig. 5. Concentrations of the analyzed elements (ppm= mg kg⁻¹) in leaves of the studied plant species at different habitats [Standard errors are shown on each column. F-values and asterisks showed the significance at: *** P< 0.001, ** P< 0.01, * P< 0.5]
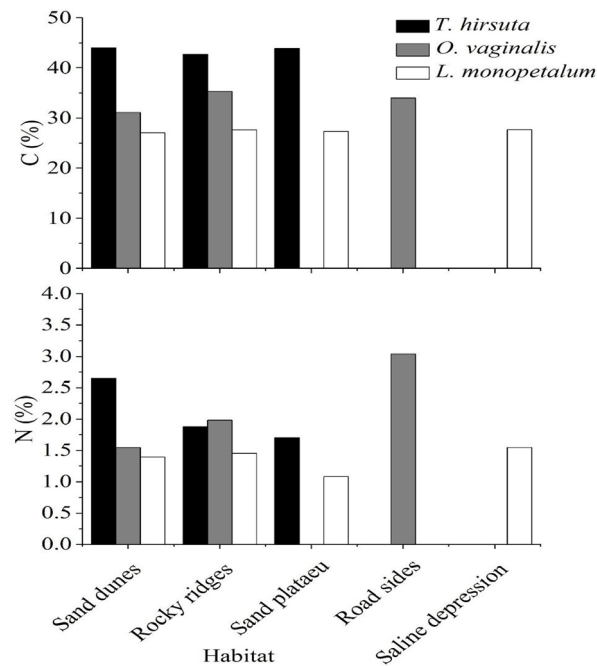

Fig. 6. Carbon and nitrogen concentrations (%) in leaves of the studied tree species at different habitats

TABLE 3. Stoichiometric (concentration) ratios in the leaves of the target plant species in the studied habitats

Habitat	C: N	C: P	N: P	K: P	C: K	Mg: P
T. hirsuta						
Sand dunes	18.1±4.3	891.7±352.7	58.6±32.1	11.9±5.2	78.5±14.6	1.1±0.2
Rocky ridges	24.4±4.9	**1420.1±376.7**	**63.4±22.3**	**16.0±3.5**	**86.7±10.2**	**1.8±0.1**
Sand plateau	**26.2±2.7**	473.1±163.6	19.7±8.8	6.2±2.6	82.8±11.7	0.8±0.4
F-value	1.1	2.3	1.1	1.6	0.1	3.1
O. vaginalis						
Sand dunes	**20.2±0.9**	610.0±117.7	29.8±4.6	8.0±1.4	**77.6±9.8**	4.3±1.5
Rocky ridges	18.1±1.7	622.3±161.2	37.0±13.6	8.5±2.4	75.9±12.2	4.9±1.7
Roadsides	12.5±2.6	**5767.2±950.9**	**485.6±73.5**	**78.6±17.7**	76.1±6.5	**36.4±8.3**
F-value	4.5	28.1***	36.5***	15.4**	0.01	13.8**
L. monopetalum						
Sand dunes	19.4±0.4	**16819.4±5272.0**	**878.4±292.1**	**455.1±137.2**	37.0±2.4	**319.22±94.8**
Rocky ridges	19.1±0.8	514.9±69.9	26.7±2.5	11.6±1.8	**44.43±1.3**	9.59±1.5
Sand plateau	**25.6±2.7**	10022.1±1658.3	412.5±100.1	257.8±57.3	39.87±2.5	155.41±33.9
Saline depression	17.9±0.3	9816.4±1919.2	552.0±119.2	292.2±60.2	33.71±1.2	195.25±38.7
F-value	5.7*	5.2*	4.5*	5.2*	5.423*	5.6*

Biochemical analyses

The phytochemicals estimated in plant leaves of *T. hirsuta* were significantly different among the studied habitats at $p < 0.05$ (Fig. 7), except SP and antioxidants. The maximum SP, antioxidants, and alkaloids concentrations were (287.7, 790.4, and 36.2 ppm) attained at sand dunes, while the sand plateau habitat attained the highest values of SC, InsC, TC, flavonoids, and phenolics, and the lowest of alkaloids. On the contrary, the lowest values of TC, flavonoids, phenolics, and antioxidants were recorded at rocky ridges, with the highest proline concentration (1.14 ppm).

For *O. vaginalis*, rocky ridges habitat had the highest mean values of Sp, SC, InsC, TC, proline, flavonoids, and phenolics but the lowest values of antioxidants and alkaloids (Fig. 7). On the other hand, roadsides had the highest mean values of antioxidants (919.2 ppm) and alkaloids (40.5 ppm) but the lowest soluble protein (99.8 ppm). All the biochemical variables of *O. vaginalis* were significantly different among the studied habitats except for antioxidants and alkaloids.

For *L. monopetalum*, the sand dune habitat attained the highest values of SP (308.6 ppm), and SC (23.2 ppm), but the lowest values of phenolics (19.9 ppm) and alkaloids (28.6 ppm) (Fig. 7). Saline depressions recorded the highest values of InsC, TC, proline, flavonoids, phenolics, and alkaloids, but the lowest values of antioxidants (554.8 ppm). In contrast, rocky ridges attained the lowest values of SC, InsC, TC, proline, and flavonoids. All the estimated biochemical variables for *L. monopetalum* were significantly different among the studied habitats except for insoluble carbohydrates.

Discussion

Soil and plant growth characteristics

Environmental variables, particularly edaphic factors, species interactions, and dispersal, influence the distribution and abundance of plant species within a specific climatic zone (Hutchings & Wijesinghe, 1997). The Western Mediterranean coast in Egypt is characterized by the presence of heterogeneous habitats that vary significantly in their physicochemical properties (Migahid et al., 1996; Migahid & Elhaak, 2001; El-Sherbeny et al., 2021). In our study area, coastal sand dunes were characterized by the highest bicarbonate content while saline depressions had the highest content of soil moisture and macronutrients. This agrees with the findings of previous studies (e.g., Migahid et al., 1996; Abd El-Maboud & Abd Elbar, 2020; El-Sherbeny et al., 2021).
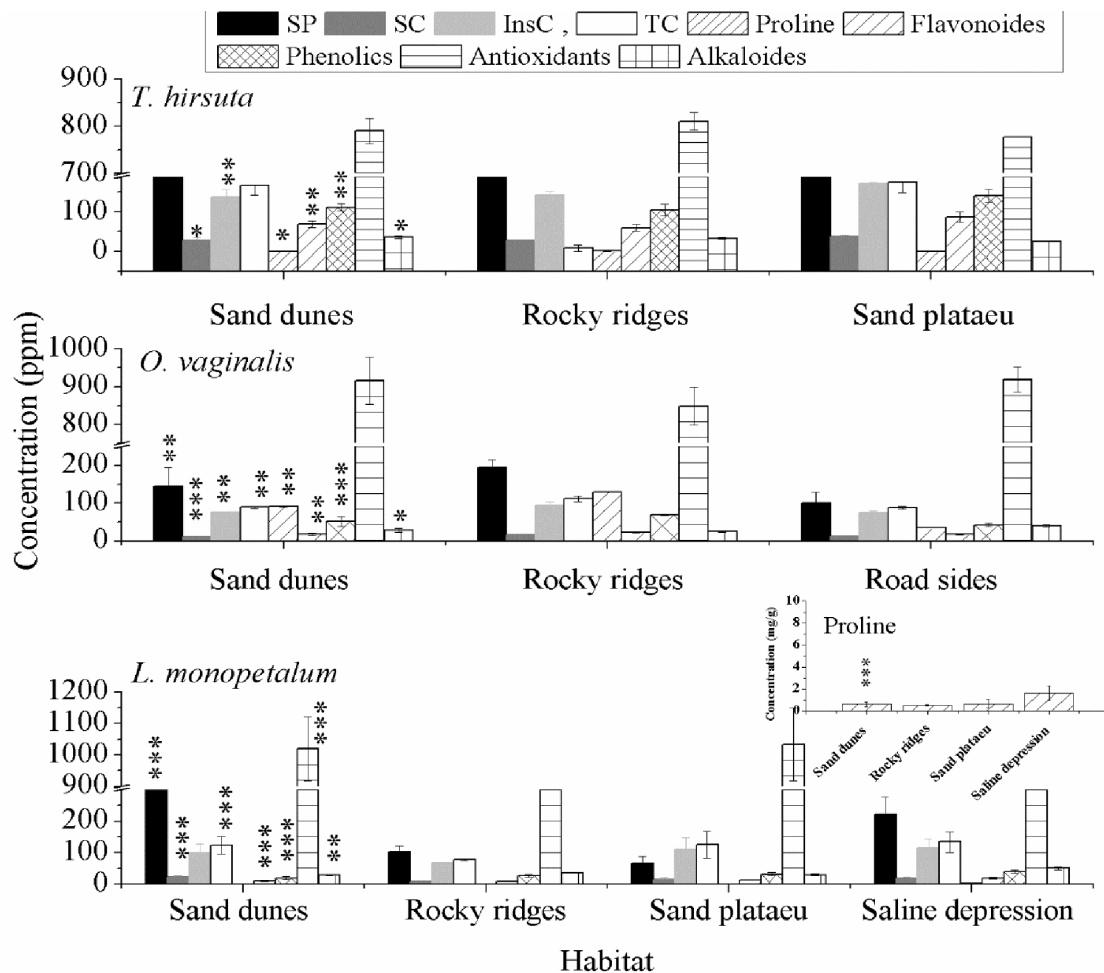
Fig. 7. Concentrations of the analyzed biochemical parameters (mg/g) in the leaves of the studied species at different habitats [Standard errors are shown on each column. Asterisks show the significance at: *** P< 0.001, ** P< 0.01, * P< 0.5. See the Methods section for abbreviations. Proline is drawn as an inset graph due to its low values in *L. monopetalum*]

In the present study, *T. hirsuta* had its highest dry matter at sand dunes and sand plateaus, which contrasts with the findings of Migahid et al. (1996) who reported the highest dry matter for the species in the rocky ridges. The absence of *T. hirsuta* from saline depression may be attributed to its sensitivity to soil salinity which negatively impacts its metabolism as reported by Migahid et al. (1996). On the other hand, *O. vaginalis* and *L. monopetalum* had their maximum dry matter at rocky ridges. This could be due to the low water content of the two species in these habitats compared to other habitats. The same was true for the stem height, and no. of branches/plant of the two species in rocky ridges compared to *T. hirsute*, which revealed the tolerance of the two species to the rocky ridges' conditions. The significant difference in the stem height and no. of branches/

plant of each species among the different habitats is indicative of the species' growth plasticity in response to the environmental conditions. This is following the findings of Hegazy et al. (2010) and Farahat et al. (2015).

Plant-soil relationships

The PCA outcomes revealed that *T. hirsuta* dominates the habitats characterized by low pH, salts, gravel, silt, and clay content, high soil moisture, bicarbonates, and coarse and medium sand content. This explains why *T. hirsuta* is common to the studied habitats except for the saline depressions, which agrees with the findings of Migahid et al. (1996). On the other hand, *O. vaginalis* grows better in soil rich in bicarbonates, coarse sand, soil gravel, and soil Fe and P content. Besides, it avoids habitats with high

nutrient contents, soil moisture, EC, fine sand, very fine sand, and clay. This coincides with the characteristics of the rocky ridges and coastal sand dunes where *O. vaginalis* attained considerable dry matter content. It can be concluded that *O. vaginalis* tolerates the high soil bicarbonates contents, alkalinity, and low nutrients prevalent in these habitats, which was also confirmed by previous studies (e.g., Abd El-Rahman & El-Monayeri, 1967; Migahid et al., 1996).

It seems that *L. monopetalum* is more influenced by the physicochemical properties of soil compared to the other two species. The strong relationship between *L. monopetalum* and soil physicochemical properties may explain its distribution in most of the habitats along the Mediterranean coast, particularly the saline depressions, and salt marshes, which was also confirmed by many investigations (e.g., Batanouny, 1993; Abd El-Maboud & Abd Elbar, 2020).

Elemental analysis and stoichiometric ratios

High macronutrient content was recorded for *T. hirsuta* and *O. vaginalis* leaves in drier habitats (coastal dunes and rocky ridges), and *L. monopetalum* in saline depression. Lower absorption of Na relative to K was detected under saline conditions, besides observing an antagonistic relationship between Na and K concentrations in all habitats for all species. The high Na and low K content in *L. monopetalum* leaves at rocky ridges are indicative of Na-induced toxicity. A similar tendency was detected for some wild plants inhabiting the Wadi El-Natrun-El-Alamein highway (Ismaeil et al., 2006), and for *L. monopetalum* in the Mediterranean coastal habitats (Abd El-Maboud & Abd Elbar, 2020). Under harsh environmental conditions, plants undergo osmoregulation through the accumulation of more inorganic ions and organic solutes. However, this depends on the ecophysiological performance of each species (Hameed & Ashraf, 2008). Habitat heterogeneity leading to high variability in chemical resources was reported to significantly influence *C. procera* leaves nutrient content (Farahat et al., 2015).

The relationships between leaf traits and the environment reflect the phenotypic plasticity of species to heterogeneous environments. Therefore, understanding these relationships is crucial for anticipating the consequences of environmental changes on plants. Studies revealed that the adaptation of species and its phenotypic responses to environmental stresses can be substantially influenced by the plant's stoichiometry, and C, N, and P concentrations (e.g., Cao et al., 2020; Zhang et al., 2020). In warm-dry and temperate-dry terrestrial ecosystems, the increase in temperature and drought was observed to raise the C: N and C: P ratios (Sardans et al., 2012). The insignificant differences among the habitats in *T. hirsuta* stoichiometric ratios indicate the tolerance to the environmental conditions in these habitats. In contrast, a significant difference in the stoichiometric ratios among the habitats of the other two species was detected. The observed C: N :P ratios exceeded that reported for terrestrial ecosystems in China (Zhang et al., 2021), and herbaceous synusia in a temperate desert in Central Asia (Tao et al., 2021). The C: N and C: P ratios detected were higher than that of the global and Loess Plateau flora reported by Tong et al. (2021) for Chinese fir in China. In contrast to the C: P, and N: P, the C: N ratio of the target species was comparable to that reported by other studies (e.g., Reich & Oleksyn, 2004; Elser et al., 2000), which can be attributed to the very low P concentrations in Egyptian soil that affects the values of the stoichiometric ratios. Studies on the Sonoran Desert (e.g., Castellanos et al., 2018), revealed that the high N, C: N, C: P, and N: P foliar stoichiometric ratios relative to other ecosystems are indicative of the P but not the N limitations in leaves.

Biochemical parameters

The impact of local habitats on the target species depends on the interaction between the species and the environmental factors prevailing in each habitat. The synthesis of secondary metabolites such as proline, soluble sugars, polyphenols, etc. in the leaves helps the plants reach osmoregulation under stress conditions. The results revealed a species-dependent response to the habitat local environmental conditions that was reflected by the variation in the content of the investigated secondary metabolites of the target species, which indicates that the species are exposed to considerable environmental stress in these habitats. For example, *T. hirsuta* attained the highest secondary metabolite content in sand formations, followed by sand dunes, then the rocky ridges, while *O. vaginalis* and *L. monopetalum* attained the maximum content in rocky ridges and saline depressions respectively. Production

of different secondary metabolites in plants is a defensive chemo-strategy under biotic and abiotic stresses (Abd El-Maboud, 2019). *L. monopetalum* was reported to accumulate a higher content of Na, K, proline, and total phenols in the leaves under salt stress (Debouba et al., 2013; Abd El-Maboud & Abd Elbar, 2020). It reveals the antioxidant defense response exhibited by the species to mitigate the destructive role of reactive oxygen species. Since the phenolic compounds including flavonoids are the most available secondary metabolites that help in signaling pathways, plant defense, mediating auxin transport, antioxidant, and free radical scavenging activities (Hodaei et al., 2018; Benabderrahmane et al., 2023).

Soluble sugars and proteins play an important protective role in osmotic regulations and act as a resource for enzymes and a modulator of metabolic processes (Zheng et al., 2018). Generally, when plants are exposed to drought or salt stress, the quantity of soluble sugars and proteins significantly increases (Watanabe et al., 2000). We think that the significant variations in the biochemical organic compounds in the target plants reflect the edaphic resource gradients in their habitats. The carbohydrate content in the target species increased in habitats away from the sea, i.e., saline depressions and rocky ridges, which is in accordance with the findings of Migahid et al. (1996). The high proline content in the tissues of *T. hirsuta* and *O. vaginalis* in rocky ridges and *L. monopetalum* in saline depressions may indicate that the local habitat conditions exert more stress on these species.

Conclusion

The distribution of the studied species was controlled mainly by soil edaphic factors that was reflected in the biochemical composition of the plants. The phenotypic plasticity of species to local habitats is species-dependent and may be controlled by the tolerance to stresses and the eco-physiological performance in reaction to environmental conditions. The significant variations in the secondary metabolites content in the target plants reflect the edaphic factors gradients in the investigated habitats. The carbohydrate content in the target species increased in habitats away from the sea. The insignificant differences among the habitats in *T. hirsuta* stoichiometric ratios indicate the species' tolerance to environmental conditions. The high

proline content in the tissues of *T. hirsuta* and *O. vaginalis* in rocky ridges and *L. monopetalum* in saline depressions may reflect stresses exerted by the local habitats' conditions on these species. The study provides a contribution towards deciphering of the plant-soil interactions and species distributions in the Mediterranean arid environments. Moreover, it revealed habitat preferences of the studied species that can be used for any future conservation or restoration program.

Conflict of interest: The authors declare that they have no conflict of interest.

Author's contributions: E. F., M.W.H and A. M. did the fieldwork and laboratory analysis, E. F.: draft the original manuscript, revised it, and submitted it to the journal; L.H. and M.W.A.H. contributed to the writing and revision of the manuscript before submission. All authors participated in the conceptualization and design layout of the work.

Ethics approval: plant materials in this study were collected and used according to national regulations. The collection and analysis of these species for research purposes do not require any special permit. All methods in our study comply with relevant institutional, national, and international guidelines and legislation. The plants were identified by the last author according to the Egyptian flora books. No vouchers for the plants were deposited at the herbarium.

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تأثير عدم تجانس الموائل على النمو والمكونات الكيمياء حيوية لثلاثة أنواع من النباتات المحلية، ساحل البحر المتوسط في مصر

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يعد فهم الأداء البيئي للنباتات الصحراوية في الموائل المختلفة أمرًا ضروريًا لأي تدابير استعادة وحفظ. تم دراسة النمو التكيفي والخصائص الكيمياء حيوية لثلاث أنواع نباتية محلية هي المثنان والشبرق والحمشد. أظهرت النتائج أن موائل المنخفضات الملحية أعطت أقصى قيم للمتغيرات المقاسة بينما موائل الكثبان الرملية أظهرت اقل القيم. اختلفت معايير النمو بشكل كبير بين موائل الأنواع المدروسة فيما عدا ارتفاع الساق وعدد الأفرع على النبات للمثنان وكان محتوي المغذيات الكبرى للأجزاء الخضرية لنبات الشبرق أعلي قيماً في الموائل الأكثر جفافاً مقارنة بنبات الحمشد. أظهرت النسب المتكافئة للعناصر اختلافا واضحاً للموائل المختلفة للنباتات الحمشد والشبرق باستثناء نسب كلا من C/N and C/K. تشير الفروق الضئيلة في النسب المتكافئة لنبات المثنان إلى مدي تحمله لظروف الإجهاد. تعكس الاختلافات الكبيرة في محتوى الأنواع من المركبات الكيميائية الحيوية التدرجات في موارد الموائل التكوينية. يشير المحتوى العالي من الكربوهيدرات في المنخفضات الملحية والتلال الصخرية إلى زيادة الإجهاد على هذه الأنواع. يوضح تحليل المكون الرئيسي (PCA) بأن نبات المثنان يسود في الموائل المنخفضة الملوحة والمحتوي العالي لرطوبة التربة والبيكربونات، والحديد، والفسفور، والرمال والحصي. بينما نبات الشبرق يفضل التربة الغنية بالبيكربونات والحديد والفوسفور والمحتوي الرملي والحصي بالتربة. يبدو أن نبات الحمشد أكثرا تأثرا بخصائص التربة مقارنةً بالأنواع الأخرى. أظهرت التفاعلات بين النبات والتربة وتوزيع الأنواع بعض الأفكار والرؤيا التي من الممكن الاستناد عليها في اختيار طرق الصون وطريق الاستخدام المستدام للأنواع في البيئات المتوسطية الجافة.