

Turkish Journal of Botany

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Spatial distribution and soil characteristics of the vegetation associated with common succulent plants in Egypt

Monier ABD EL-GHANI¹, Ashraf SOLIMAN^{1,*}, Reham ABD El-FATTAH²

¹Herbarium, Faculty of Science, Cairo University, Giza, Egypt

²Woody Trees and Forest Department, Horticultural Research Institute, Agriculture Research Center, Giza, Egypt

Received: 23.09.2013	٠	Accepted: 23.01.2014	٠	Published Online: 31.03.2014	٠	Printed: 30.04.2014
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Abstract: The most succulent species-rich family in Egypt is Chenopodiaceae, followed by Aizoaceae and then Zygophyllaceae, Crassulaceae, and Orobanchaceae. The Sinai Peninsula and the Mediterranean regions include most of these succulent species, at 73.2% and 53.7%, respectively. A floristic data matrix (59 stands and 137 species) was subjected to classification by 2-way indicator species analysis (TWINSPAN). This yielded 8 vegetation groups. The most prominent groups were the *Mesembryanthemum nodiflorum* group, the *Anabasis articulata* group, the *Zygophyllum coccineum-Zilla spinosa* group, and the *Zygophyllum album* group. The vegetation associated with the 5 most common succulent plants was analyzed, and variations in floristic composition were described. Sixteen soil physical and chemical parameters from stands dominated by each of the studied succulent plants were analyzed. This investigation demonstrated the role of 12 soil factors in affecting the distribution of the 5 studied succulent plants: electric conductivity, pH, bicarbonates, sulfates, $CaCO_3^{++}$, Ca^{++} , Mg^{++} , K^+ , Na^+ , Cl^- , silt, and sand. The application of canonical correspondence analysis indicated that the distribution of *Arthrocnemum macrostachyum* was affected by Mg and electric conductivity; *Zygophyllum album* was affected by SO₄⁺⁺, electric conductivity, and Ca⁺⁺; and *Anabasis articulata*, *Haloxylon salicornicum*, and *Zygophyllum coccineum* were highly affected by percentages of sand and clay and values of CaCO₃, total mineral nitrogen, and pH.

Key words: Egypt, multivariate analysis, soil-vegetation relationships, succulent plants, vegetation dynamics

1. Introduction

It is estimated that there are approximately 10,000 succulent plant species throughout the world, mostly found in the families Aizoaceae, Cactaceae, Crassulaceae, Euphorbiaceae, Apocynaceae, Agavaceae, Asphodelaceae Chenopodiaceae, (Aloeaceae), and Portulacaceae (Oldfield, 1997). Succulents are native to many regions from northern Europe to the Far East, although most are concentrated in southern and eastern Africa. Exploration and trading over the last 4 centuries and natural distribution enabled cacti and succulents to establish themselves in new habitats across the world (Hewitt, 1993). Cactaceae is the largest family of succulent plants, nearly endemic to North and South America, followed by Aizoaceae in South Africa. Euphorbiaceae is considered the fourth largest family among flowering plants, with over than 1000 species and worldwide distribution.

Succulents vary in shape and size from more than a few millimeters high to massive trees such as the African baobab (*Adansonia digitata* L.). Hewitt (1993) recognized 3 different habitats for succulents: 1) desert plains,

* Correspondence: ashraf-tsoliman@hotmail.com

including harsh dry habitats; (2) mountainous terrain, including high plateau, screes, and rocky slopes, where the soil is often very thin, does not retain much water, and has a high mineral content that can be toxic to nonsucculent plants; and 3) forests, where species inhabit subtropical and tropical rainforests such as those in Central and South America, Africa, Sri Lanka, and the West Indies, where the climate is constantly hot and humid and sunlight is filtered through a thick tree canopy. Economically, they can be used for medicinal (*Aloe ferox* Mill.) or mystical (*Haworthia limifolia* Marloth) purposes or as food [*Fockea edulis* (Thunberg) K.Schumann] and cordage (*Sansevieria aethiopia* Thunb.).

Studies on succulent vegetation, distribution, phytosociology, and biodiversity are universally known and include, among others, those of Böer (1996), Brown (2003), and Jafari et al. (2003) in Saudi Arabia, Kuwait, and Iran, respectively; Oguz et al. (2004) and Reineking et al. (2006) in tropical Africa; Rubio-Casal et al. (2001) and Curco et al. (2002) in the Mediterranean Basin; and Rebman (2001) in the Americas. In Egypt, some similar

studies were carried out, e.g., those of Serag et al. (1998), El Shayeb et al. (2002), and Salama and Ali (2003) on the Mediterranean coast of Egypt and Shaltout et al. (2003) and Abd El-Ghani and Amer (2003) on the Red Sea coast and the Sinai Peninsula. Moreover, the works of Abd El-Ghani et al. (2013) and Salama et al. (2013) in Egypt and Abdel Khalik et al. (2013) in Saudi Arabia are among most recent studies conducted that highlight the importance of the application of numerical methods such as cluster and correlation analyses and multivariate techniques such as correspondence analyses to express the relationships between weed species and relevant habitats.

From a preliminary study of the literature and herbaria reviews, the succulents are represented by 82 plant species in Egypt. These can be classified into 59 leafy succulents (e.g., *Zygophyllum coccineum* L. and *Mesembryanthemum crystallinum* L.) and 23 stem succulents [e.g., *Arthrocnemum macrostachyum* (Moric.) C.Koch and *Anabasis articulata* (Forssk.) Moq.]. Generally, the biological spectrum of the succulent species in Egypt includes 35 shrubs, 18 perennial herbs, and 29 annuals.

This study aims to identify the geographical distribution patterns of succulent plants in Egypt and to assess the aspects of floristic diversity and vegetation composition associated with the 5 selected most common succulent desert plants in relation to the prevailing soil factors.

2. Materials and methods

2.1. Vegetation sampling

Between 2004 and 2007, an extensive survey was carried out at 13 different georeferenced sites representing 6 phytogeographic regions in Egypt (Wickens, 1977). A total of 59 stands (20×20 m), georeferenced using a Trimble SCOUT GPS model, were randomly chosen in the 13 sites to represent the apparent variation in the different habitats, distributed as follows: 14 in the Nile region, 9 along the western Mediterranean coast, 18 in the Sinai Peninsula North and South, 13 along the Red Sea coast, and 5 in the Eastern Desert (Figure 1). In each of the studied stands, ecological notes and presence or absence of plant species were recorded. The line intercept technique (Canfield, 1941) was applied to estimate the cover of the species recorded. In order to perform this analysis, a measuring tape of 20 m in length was laid out on the ground and the crowns that overlapped or intercepted the lines were calculated. This was carried out 5 times for each stand such that a total of 100 m of length was monitored. The presence (P%) was calculated as the number of stands where species were recorded divided by the total number of stands \times 100. Identification of species was carried out at the herbarium of Cairo University (CAI). Taxonomic nomenclature was according to Täckholm (1974) and Boulos (1995, 1999, 2000, 2002, 2005, 2009).

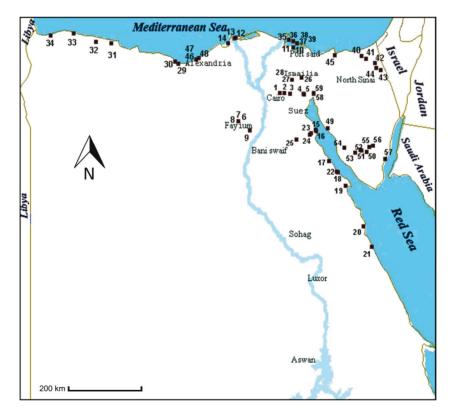


Figure 1. Map showing the distribution of the 59 studied stands.

2.2. The selected species

Among the 21 succulents recorded during this study, 5 species were found to be of common occurrence. *Anabasis articulata* (Forssk.) Moq., *Zygophyllum coccineum* L., and *Haloxylon salicornicum* (Moq.) Bunge ex Boiss. were among the xerophytic succulents, while *Arthrocnemum macrostachyum* (Moric.) C.Koch is a halophytic succulent and *Zygophyllum album* L. is a haloxerophytic succulent (Hassib, 1951).

2.3. Soils sampling and analysis

Soils samples were collected from each stand at 3 depths: 0-10, 10-25, and 25-50 cm. The samples were pooled together to form one composite sample, spread over sheets of paper, and left to dry in the air. Dried soils were passed through a 2-mm sieve to remove gravel and debris, and were then packed in paper bags for physical and chemical analyses. Soil textural analysis was determined by the hydrometer analysis method, and the results were used to calculate the percentages of sand, silt, and clay. The soil textural classes were determined by textural triangle diagram, and calcium carbonate content was determined volumetrically using Collin's calcimeter apparatus. Soluble bicarbonates were determined according to Page et al. (1982). Soil extracts were prepared and then used in order to determine chemical analysis. Soil reaction (pH) was measured in soil-water extract (1:2.5) using a Beckman pH meter. The electrical conductivity (EC) was measured in soil-water extract (1:5) using a conductivity meter. Sulfates were determined gravimetrically and the soluble sulfates were precipitated as barium sulfates. Sodium and potassium ions were determined using a flame photometer. Calcium and magnesium ions were determined by titration with EDTA. The estimation of chlorides in the soil extract was carried out by titration method against silver nitrate (AgNO₃) using potassium chromate (K₂Cr₂O₇) as an indicator. Total mineral nitrogen including ammonia and nitrate in soil was determined using the Kjeldahl method. Available phosphorus was determined by the Olsen method. Available potassium in the soil was extracted with ammonium acetate and measured with a flame photometer. The method of Jackson (1973) was used for all analysis techniques.

2.4. Data analysis

Classification and ordination of the associated vegetation of the studied succulent plants were performed using presence/absence data. For this purpose, a floristic data matrix (the monitored 59 stands and the recorded 137 recorded species) was subjected to classification by 2-way indicator species analysis (TWINSPAN) using the default settings of the computer program PC-ORD for Windows, version 4.14 (McCune and Mefford, 1999). TWINSPAN is a FORTRAN program for arranging multivariate data in an ordered 2-way table by classification of the stands and species. An ordered 2-way table that expresses succinctly the relationships of the stands and species within the data set was constructed. Indicator species refer to the preferential species used by TWINSPAN to distinguish the sample groups. The stands are ordered first by divisive hierarchical clustering, and then the species are clustered based on the classification of stands (Gauch and Whittaker, 1981).

Preliminary analysis using the default options of detrended correspondence analysis (DCA; Hill and Gauch, 1980) in the CANOCO program, version 4.0 for Windows (Ter Braak and Šmilauer, 1998), was applied to check the magnitude of change in species composition along the first ordination axis (i.e. gradient length in standard deviation units). DCA estimated that the compositional gradient in the vegetation data ranged from 4 to 10 standard deviation units for most subset analyses and thus was the appropriate ordination method to perform direct gradient analysis (Ter Braak and Prentice, 1988). Direct gradient analysis is that in which species composition is directly and immediately related to measured environmental variables (Ter Braak, 1986). In CANOCO, the relationships between vegetation gradients and the studied environmental variables can be indicated on the ordination diagram produced by the canonical correspondence analysis (CCA) biplot. Each arrow determines an axis upon which the species points can be projected. The exploratory CCA was evaluated using interest correlations and CCA axes were evaluated statistically by means of a Monte Carlo permutation test (499 permutations; Ter Braak and Prentice, 1988).

All data variables were assessed for normality (SPSS 17.0 for Windows) prior to the CCA analysis, and appropriate transformations were performed when necessary to improve normality according to Zar (1984). Sixteen environmental variables were included in this study: soil reaction (pH), EC, calcium carbonate (CaCO,), bicarbonates (HCO,), chlorides (Cl-), sulfates (SO, ²), calcium (Ca⁺²), magnesium (Mg⁺²), sodium (Na⁺), potassium (K⁺), total mineral nitrogen (N), phosphorus (P), available potassium (aK), sand, silt, and clay. Due to high inflation factors for Na⁺, aK, and Cl⁻, they were excluded from the CCA analysis. The TWINSPAN vegetation groups were subjected to one-way analysis of variance (ANOVA) based on soil variables to find out whether there were significant variations among groups. Analysis of variance provides an insight into the nature of variation of natural events, which is possibly of even greater value than the knowledge of the method as such (Sokal and Rohlfs, 1981). Species richness (SR) within each separated TWINSPAN vegetation group was calculated as the average number of species per stand. The Shannon-Wiener diversity index was calculated from the formula H'= $-\Sigma Pi \ln Pi$ (Pielou, 1975), where *H*' is Shannon–Wiener diversity index and Pi is the relative cover of the *i*th species.

3. Results

3.1. Distribution patterns of succulents

The Appendix shows the distribution of the succulent flora in the different phytogeographic regions of Egypt. The Sinai Peninsula and the Mediterranean regions included most of the succulent species: 60 species (73.2%) in 11 families in the Sinai, and 44 species (53.7%) in 14 families in the Mediterranean region. The most species-rich succulent family is Chenopodiaceae (28 species), followed by Aizoaceae (10 species) and then Zygophyllaceae (6 species), Crassulaceae, Orobanchaceae, and Tamaricaceae (5 species each). The best represented genera are *Suaeda* (9 species), *Zygophyllum* (5 species), *Salsola* and *Caralluma* (4 species each), and *Mesembryanthemum* and *Euphorbia* (3 species for each).

Species varied according to their affinities in the different phytogeographic regions. Only *Hyoscyamus muticus* and *Arthrocnemum macrostachyum* were represented in all 7 phytogeographic regions. *Suaeda vera*, *S. vermiculata*, and *Cistanche phelypaea* were represented in 6 regions each, exhibiting a wide geographical and ecological range of distribution. Some species showed a certain degree of consistency, i.e. were confined to a certain phytogeographic region. Ten species were confined to Gebel Elba, such as the perennial herb *Caralluma acutangula*, while the perennial shrubs *Haloxylon negevensis* and *Umbilicus rupestris* were confined to Sinai and the annual *Suaeda altissima* and the salt marsh subshrubs *Suaeda palaestina* and *Tetradiclis tenella* were confined to the Mediterranean region.

From an attempt to compare the floristic composition of succulent plants of arid regions in countries neighboring

Egypt, Table 1 shows that the most succulent speciesrich families were Chenopodiaceae, Aizoaceae, and Zygophyllaceae, respectively. In Sudan, Euphorbiaceae (6 species) ranked second to Chenopodiaceae (7 species). It was also obvious that Egypt had the highest number of succulents (82 species), followed by Palestine and Saudi Arabia (51 species for each), Libya (48 species), and Sudan (47 species).

3.2. Spatial distribution patterns of the studied succulents In this study, a total of 137 species of vascular plants were recorded, belonging to 37 families. They consisted of 1 tree (*Tamarix nilotica*), 57 shrubs and subshrubs constituting the largest portion of the collected flora (41.6%), 30 herbaceous perennials representing 21.9%, 2 biennials, and 47 annuals representing 34.3% of the recorded species. The most species-rich families were Chenopodiaceae (24) and Asteraceae (23), representing 17.5% and 16.8% of the total collected flora, respectively, followed by Zygophyllaceae and Poaceae (10 each), Brassicaceae and Fabaceae (7 each), Polygonaceae (5), and Aizoaceae and Boraginaceae (4 each).

Regarding 5 the most common succulent species, *Anabasis articulata* was collected from 13 of the 59 studied stands (Figure 2) in 4 of the 6 selected regions as follows: 3 from the Red Sea region, 3 from the western Mediterranean region, 4 from the North Sinai region, and 3 from the South Sinai region. *Zygophyllum album* was collected from 15 stands as follows: 4 from the Nile region, 5 from the Red Sea coastal region, 2 from the Eastern Desert region, 1 from the western Mediterranean coastal region, and 3 from the North Sinai region (Figure 2). *Haloxylon salicornicum* was

Table 1. Numbers of succulent species in different families in the flora of Egypt as well as other adjacent countries for comparison. Sources: 1 = Boulos (1999, 2000, 2002, 2005); 2 = Zohary (1966, 1972) and Feinbrun-Dothan (1978, 1986); 3 = Migahid (1996); 4) Flora of Libya (different families); 5 = Andrews (1950, 1952, 1956).

Families	Egypt ¹	Palestine ²	Saudi ³ Arabia	Libya ⁴	Sudan ⁵
Chenopodiaceae	28	20	18	16	7
Aizoaceae	10	6	7	8	4
Zygophyllaceae	6	4	3	3	3
Crassulaceae	5	3	2	3	3
Orobanchaceae	5	3	2	3	1
Tamaricaceae	5	4	1	2	0
Asclepiadaceae	4	2	3	1	4
Euphorbiaceae	3	0	2	0	6
Portulacaceae	3	3	2	2	3
Commelinaceae	2	0	3	3	1
Other families	11	6	8	7	15
All species	82	51	51	48	47

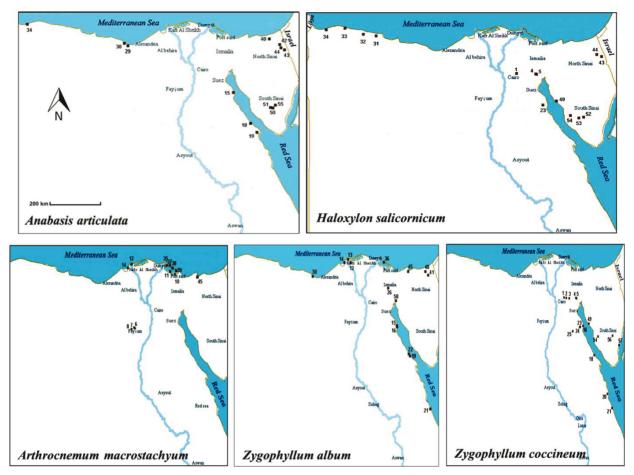


Figure 2. Distributional patterns of the 5 studied succulents showing their monitored stands.

collected from 14 stands (Figure 2) in 4 of the 6 selected phytogeographic regions: 4 from the Eastern Desert region, 4 from the western Mediterranean coastal region, 2 from the North Sinai region, and 4 from the South Sinai region. Monospecific stands were detected in stand 31 of the western Mediterranean coast and in stand 52 in South Sinai. *Zygophyllum coccineum* was collected from 16 stands (Figure 2) in 3 phytogeographic regions: 8 in the Eastern Desert region, 4 in the Red Sea coastal region, and another 4 in the South Sinai region. *Arthrocnemum macrostachyum* was collected from 12 stands (Figure 2) in 2 phytogeographic regions: 11 from the Nile region and 1 from the North Sinai region. Monospecific stands were detected in stands 7 and 8, both in the Fayium area, an oasis connected to the Nile by an irrigation canal.

3.3. Classification of the associated vegetation

The TWINSPAN classification of 59 stands resulted in 8 vegetation groups (A–H; Table 2) at the third level of hierarchical classification. A dendrogram is depicted in Figure 3, along with the indicator species that characterize the stand groups. The 8 vegetation groups were named after their characteristic species (having the highest presence values) as follows: Group A, Mesembryanthemum crystallinum-Mesembryanthemum nodiflorum; Group B, Haloxylon salicornicum-Polygonum equisetiforme-Deverra tortuosa-Carduncellus mareoticus; Group C, Anabasis articulata; Group D, Zygophyllum coccineum-Zilla spinosa; Group E, Zygophyllum album; Group F, Zygophyllum album-Senecio glaucus; Group G, Arthrocnemum macrostachyum; and Group H, Tamarix nilotica. Table 3 displays the variations in soil characteristics among the identified TWINSPAN vegetation groups. Clearly, 9 soil parameters were highly significant (P \leq 0.01), and 4 showed significant differences (P \leq 0.05). Species richness (SR) was also highly significant among the groups.

3.3.1. Group A: Mesembryanthemum crystallinum-Mesembryanthemum nodiflorum group

This group comprised 22 species in 3 stands located in Burg El-Arab, along the western Mediterranean region. The soil was loamy sand with the highest values of soil reaction (pH), calcium carbonates, and potassium; high content of bicarbonates; very low values of salinity, chlorides, and sulfates; and the lowest calcium content (Table 3). Five common associated species (P = 66.7%) were recognized,

Table 2. Characteristic species of the 8 TWINSPAN groups (A–H) with their presence values (P%). Figures in bold are the dominant
species with the highest values.

ГWINSPAN Groups	А	В	С	D	E	F	G	Η
Total number of stands	3	3	18	15	6	3	8	3
Total number of species	22	21	52	48	17	17	14	17
Mesembryanthemum crystallinum L.	100					66.7		
Mesembryanthemum nodiflorum L.	100							
Bassia muricata (L.) Asch.	66.7			20		33.3	12.5	
Schismus barbatus (L.) Thell.	66.7			13.3				
Asphodelus aestivus Brot.	66.7	33.3						
Polygonum equisetiforme Sm.	66.7	100						
Deverra tortuosa (Desf.) DC.	33.3	100	5.6	6.7				
Haloxylon salicornicum (Moq.) Bunge ex Boiss.		100	33.3	33.3				
Carduncellus mareoticus (Delile) Hanelt		100	16.7	13.3				
Thymelaea hirsuta (L.) Endl.	66.7	66.7	16.7					
Echinops spinosus L.		66.7		6.7				
Anabasis articulata (Forssk.) Moq.			66.7		16.7			
Fagonia mollis Delile			33.3	6.7				
Zygophyllum coccineum L.			16.7	86.7				
<i>Zilla spinosa</i> (L.) Prantl			27.8	66.7				
Zygophyllum simplex L.				53.3				
Pulicaria undulata (L.) C.A.Mey. subsp. undulata			11.1	46.7				
Fagonia arabica L.			22.2	33.3				
Zygophyllum album L.			27.8	6.7	100	100		
Tamarix nilotica (Ehrenb.) Bunge				6.7	50	33.3	12.5	100
Halocnemum strobilaceum (Pall.) M.Bieb.					50	33.3	37.5	
Cistanche phelypaea (L.) Cout.					33.3			
Senecio glaucus L.			5.6		33.3	100	12.5	
Limbarda crithmoides (L.) Dumort.					16.7	66.7	12.5	33.3
Bromus rubens L.						66.7		
Hordeum murinum L. subsp. glaucum (Steud.) Tzvelev						66.7		
Arthrocnemum macrostachyum (Moric.) K.Koch					33.3	33.3	100	33.3
Phragmites australis (Cav.) Trin. ex Steud.					16.7	66.7	75	33.3
Suaeda aegyptiaca (Hasselq.) Zohary							37.5	
uncus rigidus Desf.						66.7	12.5	66.7
Alhagi graecorum Boiss.			5.6				12.5	33.3
Symphyotrichum squamatum (Spreng.) Nesom			5.6					33.3
Zygophyllum aegyptium Hosny			5.6					33.3

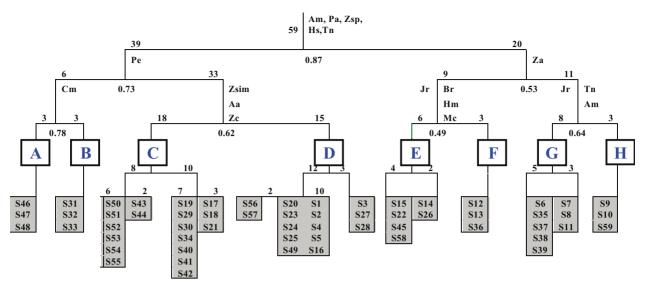


Figure 3. TWINSPAN classification of the 59 stands in the study areas, showing the 8 TWINSPAN vegetation groups (A–H) at the third hierarchical level of classification. Indicator species: Am = Arthrocnemum macrostachyum, Pa = Phragmites australis, Zsp = Zilla spinosa, Hs = Haloxylon salicornicum, Tn = Tamarix nilotica, Pe = Polygonum equisetiforme, Za = Zygophyllum album, Cm = Carduncellus mareoticus, Aa = Anabasis articulata, Zsim = Zygophyllum simplex, Zc = Zygophyllum coccineum, Mc = Mesembryanthemum crystallinum, Br = Bromus rubens, Hm = Hordeum murinum subsp. glaucum, Jr = Juncus rigidus.

including Bassia muricata, Polygonum equisetiforme, and Thymelaea hirsuta.

3.3.2. Group B: Haloxylon salicornicum-Polygonum equisetiforme-Deverra tortuosa-Carduncellus mareoticus group

This group comprised 21 species in 3 stands located in the western Mediterranean coastal region. The soil was characterized by the highest contents of bicarbonates and total mineral nitrogen, high contents of calcium carbonates and silt, and the lowest contents of pH and sulfates. *Haloxylon salicornicum*, *Polygonum equisetiforme*, *Deverra tortuosa*, and *Carduncellus mareoticus* were the dominant species (P = 100%). *Thymelaea hirsuta* and *Echinops spinosus* were the codominant species at P = 66.7%.

3.3.3. Group C: Anabasis articulata group

This group comprised 52 species in 18 stands located in 4 different regions: the Red Sea coast, the western Mediterranean coast, and North and South Sinai. The soil was characterized by the lowest contents of potassium and phosphorus with low sodium contents. Shrubs *Haloxylon salicornicum* and *Fagonia mollis* showed moderate presence (P = 33.3%).

3.3.4. Group D: Zygophyllum coccineum-Zilla spinosa group

This group comprised 48 species in 15 stands located in 3 different regions: the Red Sea coast, the Eastern Desert, and South Sinai. The soil was characterized by high contents of sand and calcium carbonates and low values of potassium

and bicarbonates. The EC and magnesium, sodium, and chloride contents were the lowest among all groups. The common associated species were *Zygophyllum simplex* (P = 53.3%, recorded in 8 stands) and *Pulicaria undulata* subsp. *undulata* (P = 46.7%, recorded in 7 stands).

3.3.5. Group E: Zygophyllum album group

This group comprised 17 species in 6 stands located in the salt marshes of the Nile region (Lake Idku), Red Sea coastal region, Eastern Desert region, and North Sinai region. The soil was sandy with the lowest silt contents and characterized by the highest contents of magnesium, sodium, and sulfates and high values of electric conductivity and calcium. The salinity content of the soil favors the growth of some halophytic species such as *Zygophyllum album*, *Tamarix nilotica*, *Halocnemum strobilaceum*, and *Limbarda crithmoides*. *Zygophyllum album* was the dominant species of this group.

3.3.6. Group F: *Zygophyllum album-Senecio glaucus* group This group comprised 17 species in 3 stands located in the salt marshes of the Nile region (Lake Burullus and Dumyat). The soil was characterized by the lowest contents of calcium carbonate, bicarbonates, and total mineral nitrogen. The associated vegetation encompassed high presence values (P = 66.7%), such as *Limbarda crithmoides*, *Phragmites australis*, and *Mesembryanthemum crystallinum*.

3.3.7. Group G: Arthrocnemum macrostachyum group

This group comprised 14 species in 8 stands located in the salt marshes of the Nile region (El-Fayium, Lake Manzala, and Dumyat). The soil was characterized by the

	T	TWINSPAN Groups	roups							
SOIL VALIADIES	lotal Mean	A	В	С	D	н	F	G	Н	Р
pH	8.36 ± 0.5	9.03 ± 0.7	7.9 ± 0.26	8.44 ± 0.64	8.27 ± 0.37	8.12 ± 0.29	8.33 ± 0.25	8.68 ± 0.33	7.9 ± 0.52	0.03 *
EC	3.98 ± 8.0	0.79 ± 0.4	1.31 ± 0.86	1.2 ± 1.68	0.7 ± 0.45	11.02 ± 16.23	3.8 ± 3.4	10.45 ± 11.25	11.81 ± 12.4	0.006 **
CaCO ₃ (%)	20.21 ± 20.9	45.73 ± 30.0	38.8 ± 23.59	23.61 ± 23.56	21.7 ± 17.1	12.47 ± 19.02	2.23 ± 1.54	9.68 ± 13.22	9.8 ± 2.31	0.054
Ca ⁺²	7.38 ± 10.1	1.1 ± 0.6	2.07 ± 1.7	3.75 ± 5.37	3.49 ± 4.27	18.62 ± 16.82	13.2 ± 10.5	10.64 ± 11.47	23.2 ± 12.1	0.000 **
Mg^{+2}	5.55 ± 8.8	1.43 ± 1.4	4.53 ± 3.23	3.14 ± 3.96	1.27 ± 0.86	13.48 ± 15.84	6.2 ± 4.39	10.38 ± 11.37	17.267 ± 17.3	0.005 **
Na^+	28 ± 73.3	4.07 ± 2.9	6.28 ± 3.73	4.2 ± 8.19	1.85 ± 1.37	91.55 ± 170.9	20.39 ± 22.29	83.7 ± 93.12	79.1 ± 105.9	0.025 *
K + (mEq/L)	0.71 ± 0.9	0.86 ± 0.4	0.49 ± 0.10	0.31 ± 0.19	0.33 ± 0.21	1.04 ± 1.38	0.8 ± 0.6	1.94 ± 1.86	1.11 ± 0.79	0.003 **
HCO ₃ -	1.21 ± 0.5	1.53 ± 0.8	2.6 ± 0.78	1.24 ± 0.49	1 ± 0.25	1.05 ± 0.28	0.87 ± 0.15	1.09 ± 0.35	1.43 ± 0.71	0.001 **
CI -	26.5 ± 6.6	2.65 ± 2.3	8.5 ± 6.06	6.82 ± 10.21	1.92 ± 1.32	73.9 ±135.8	12.58 ± 13.37	77.81 ± 90.45	90.7 ± 132.1	0.023 *
SO_4^{-2}	14.1 ± 28.6	3.38 ± 2.5	2.27 ± 2.54	3.62 ± 6.66	3.99 ± 5.40	49.8 ± 66.9	27.1 ± 39.2	27.89 ± 29.59	28.8 ± 6.2	0.006**
Z	21.5 ± 15.1	15.7 ± 0.58	30.7 ± 34.1	23.7 ± 16.9	18.1 ±12.3	21.8 ± 11.1	13.3 ± 7.6	22.3 ± 17.6	28.3 ± 7.6	0.780
P (ppm)	18.7 ± 9.4	28.7 ± 7.0	17.7 ± 10.1	14.1 ± 7	20.7 ± 12.3	21.2 ± 11.4	20.3 ± 0.58	19.6 ± 4.6	18.7 ± 11.4	0.252
aK	260.4 ± 243.2	328 ± 160.6	325.3 ± 120.4	166.7 ± 101.2	148.9 ± 43.2	248 ± 238	269.3 ± 233.1	555 ± 430.9	477.3 ± 354.3	0.002 **
Sand	86.3 ± 9.8	85.8 ± 0.6	80.6 ± 11.02	88 ± 7.8	89.3 ± 3.7	92.9 ± 3.2	87.3 ± 6.1	78.8 ± 17.4	73.3 ± 13.5	0.019 *
Silt (%)	6.31 ± 8.5	6.3 ± 0.58	13.3 ± 9.2	5.1 ± 4.1	2.6 ± 1.35	1.17 ± 1.33	4 ± 3.46	14.04 ± 16.55	17.3 ± 14.01	0.003 **
Clay	7.37 ± 3.3	7.9 ± 0.00	6.1 ± 2.0	6.95 ± 4.03	8.05 ± 3.25	5.95 ± 3.22	8.68 ± 4.08	7.13 ± 3.11	9.34 ± 0.59	0.782
SR	15.92 ± 0.3	15.67 ± 0.58	16 ± 0	15.94 ± 0.24	16 ± 0	15.5 ± 0.55	16 ± 0	16 ± 0	16 ± 0	0.004**
H'	1.6 ± 0.2	1.4 ± 0.28	1.46 ± 0.13	1.59 ± 0.3	1.6 ± 0.12	1.83 ± 0.29	1.63 ± 0.18	1.53 ± 0.23	1.7 ± 0.44	0.262

groups obtained by TWINSPAN in the study areas. PH = soil reaction, EC = electric conductivity, $CaCO_3 = calcium$ carbonate, $Ca^{+2} = calcium$, $Mg^{+2} = magnesium$, $Na^+ = sodium$, $K^+ = potassium$, $HCO_2 = bicarbonates$, CI = chloride, $SO_2^{-2} = sulfates$, N = total mineral nitrogen, P = phosphorus, aK = available potassium. *: $P \le 0.05$, **: $P \le 0.01$. Table 3. Mean values, standard deviations, and ANOVA P-values of the soil variables, species richness (SR). and Shannon's index (H') in the stands representing the 8 vegetation

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Table 4. Interset correlations of the soil variables along the first 3 axes of CCA, together with their eigenvalues, species–environment correlations, and cumulative % variance of species–environment relations. For units and abbreviations, see Table 3.

Axes	Ax1	Ax2	Ax3
Eigenvalues	0.48	0.26	0.16
Species-environment correlation	0.74	0.64	0.48
Cumulative % variance of species- environment relation	51.00	78.50	94.80
pН	0.17	-0.26	0.06
EC	0.33	0.14	0.10
CaCO ₃	-0.38	-0.05	-0.10
Ca ⁺²	0.25	0.31	0.01
Mg^{+2}	0.31	0.22	0.12
HCO ₃	-0.02	-0.22	0.28
SO ₄ -2	0.28	0.21	0.09
Ν	-0.03	-0.20	0.21
Р	0.10	0.07	-0.04
K+	0.57	-0.12	0.04
Sand	-0.31	0.34	-0.01
Silt	0.39	-0.32	0.04
Clay	-0.06	-0.20	-0.04

highest values of potassium; high contents of pH, sodium, chlorides, and silt; and low content of calcium carbonates. *Phragmites australis* was the codominant species of this group (P = 75%).

3.3.8. Group H: Tamarix nilotica group

This group comprised 17 species in 3 stands located in the salt marshes of the Nile and Eastern Desert regions. The soil was characterized by the highest values of EC, calcium, chlorides, and silt; high contents of magnesium, potassium, and sulfates; and the lowest content of sand. *Juncus rigidus* was the codominant species of this group (P = 66.7%).

3.4. Species-soil relationships of the studied succulents

The successive decrease of the eigenvalues of the first 3 CCA axes (Table 4) suggests a well-structured data set. The species–environment correlations are higher for the first 3 canonical axes, however, explaining 94.8% of the cumulative variance. These results suggest an association between vegetation and the measured soil parameters presented in the triplot (Jongman et al., 1987). A test for significance with an unrestricted Monte Carlo permutation test (499 permutations) found the F-ratio for the eigenvalue of axis 1 and the trace statistic to be significant (P < 0.002), indicating that the observed patterns did not

arise by chance. From the interset correlations of the soil factors with the first 3 axes of CCA (Table 4), it can be noted that CCA axis 1 is highly positively correlated with K^+ and highly negatively correlated with $CaCO_3$. This can be seen more clearly in the ordination triplot (Figure 4). This axis can be defined as the aK–CaCO₃ gradient. CCA axis 2 is highly positively correlated with sand and highly negatively correlated with silt. This axis can be defined as the sand–silt gradient.

The information shown in Figure 4 also indicates that the distribution of *Arthrocnemum macrostachyum (Art mac)* was affected by Mg and EC, assigned to vegetation group (G). The distribution of *Zygophyllum album (Zyg alb)*, which was assigned to groups (E) and (F), was affected by SO₄, EC, and Ca. *Anabasis articulata, Haloxylon salicornicum*, and *Zygophyllum coccineum* were assigned to groups (C), (B), and (D), respectively. These species were highly affected by percentages of sand and clay and values of CaCO₃, N, and pH.

4. Discussion

Application of multivariate analysis techniques helped to classify the vegetation associated with the studied succulent plants into 8 vegetation groups. The most prominent, Zygophyllum album (Group E), is widely distributed among 4 phytogeographic regions, the Nile, Red Sea, Sinai, and Eastern Desert. It can also be noted that certain vegetation groups are linked to definite phytogeographical regions: the Mesembryanthemum crystallinum-Mesembryanthemum nodiflorum group (Group A) and Haloxylon salicornicum-Polygonum equisetiforme-Deverra tortuosa-Carduncellus mareoticus group (Group B) are recorded from the Mediterranean region, while Zygophyllum album-Senecio glaucus (Group F) and Arthrocnemum macrostachyum (Group G) are recorded from the Nile region only. This investigation demonstrated the role of 12 soil factors in affecting the distribution of the 5 studied succulent plants: EC, pH, bicarbonates, sulfates, CaCO3++, Ca++, Mg++, K+, Na⁺, Cl⁻, silt, and sand.

The soil reaction in the Egyptian desert is alkaline. The recorded pH values in the stands of this investigation were in the range of 7.4 to 9.7. This is consistent with the results of Abd El-Wahab et al. (2006) in South Sinai.

Earlier studies recognized the *Arthrocnemum macrostachyum* group, e.g., Kassas and Zahran (1967) in the littoral salt marshes of the Red Sea coast; Abd El-Ghani (2000) in the Siwa Oasis; Mashaly (2001) in the western sector of the deltaic Mediterranean coast of Egypt; Ramadan (2002) in Lake Manzala, Egypt; and Abd El-Ghani and El-Sawaf (2005) in the saline depressions along El Arish and Rafah road verges (North Sinai).

Galal and Fawzy (2007) recognized the *Chenopodium* murale-Mesembryanthemum crystallinum group in the

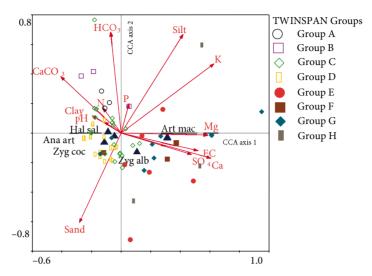


Figure 4. CCA ordination triplot of the 5 studied succulent plants (solid triangles), stands, and soil variables, reflecting distributions of the 5 succulent plants along gradients of soil variables. *Art mac* = *Arthrocnemum macrostachyum*, *Hal sal* = *Haloxylon salicornicum*, *Ana art* = *Anabasis articulata*, *Zyg alb* = *Zygophyllum album*, and *Zyg coc* = *Zygophyllum coccineum*.

interdune areas of black sand dunes in the northern Nile Delta. The present study showed that the group dominated by *Mesembryanthemum crystallinum* inhabited soil with high values of sand, carbonates, pH, and K and low contents of salinity, chlorides, and sulfates. This partly agrees with the results obtained by El Shayeb et al. (2002), who indicated the sandy halophytic nature of this group, and Galal and Fawzy (2007), who distinguished this group by its high soil contents of sulfates, calcium, magnesium, sodium, and potassium.

Anabasis articulata is one of the common desert succulent chenopods that are capable of building phytogenic mounds in various phytogeographical territories of Egypt, demonstrating wide ecological amplitude. This study revealed that the Anabasis articulata group is the most diversified (52 species) among other recognized vegetation groups. This vegetation group inhabited the limestone formations of the Eastern Desert (Kassas and Girgis, 1965; El Adawy, 2001) and the salt marshes of the western Mediterranean desert (Ayyad and E1-Ghareeb, 1982). This study also showed that soils with higher values of calcium carbonate, pH, and sand have the characteristic edaphic conditions associated with the Anabasis articulata group. This result is similar to those of other relevant studies (Baayo, 2005). It has been repeatedly recorded in many parts of the country, e.g., the Cairo-Suez desert (Kassas and El-Abyad, 1962), the Helwan Desert (Girgis, 1962), the coastal plain of the Gulf of Suez and in Wadi El-Tor of South Sinai (Zahran and Willis, 1992), Wadi Qena of the Eastern Desert (Zahran et al., 1995), and the gravel plains at the foot of the Diffa plateau in the Sallum and Sidi Barani areas of the western Mediterranean coast of Egypt (Salama et al., 2005). Outside of Egypt, it was also found in Wadi Al-Ammaria in Saudi Arabia (Alyemeni, 2001) and in the Cholistan desert in Pakistan (Arshad et al., 2008). This study identified the vegetation group of *Haloxylon salicornicum-Deverra tortuosa-Polygonum equisetiforme-Carduncellus mareoticus*, which was not recorded earlier. It inhabited soil with high contents of calcium carbonate and sand and low contents of salinity. This result is in line with other relevant studies (Alyemeni, 2001; Arshad et al., 2008; Shaltout et al., 2008).

On the other hand, Zygophyllum coccineum is a widespread xerosucculent inhabiting the drainage channels of the limestone desert, and in this investigation it formed a distinct vegetation group, Zygophyllum coccineum-Zilla spinosa, in the Red Sea coastal lands, Eastern Desert, and South Sinai. Shaltout et al. (2004) identified Zygophyllum coccineum-Zilla spinosa communities along the Egyptian Red Sea coastal lands. Several studies recognized Zygophyllum coccineum as a community associated with Zilla spinosa (Kassas and El-Abyad, 1962; Kassas and Girgis, 1965; Abd El-Ghani, 1998). Monotypic communities of the dominant species were recorded (Fossati et al., 1998). This study demonstrated that the Zygophyllum coccineum-Zilla spinosa vegetation group is mainly characterized by soil rich

in sand contents and calcium carbonates, with low values of salinity. The results of this work are consistent with those of other similar studies (Shaltout and El-Sheikh, 2002; Hegazy et al., 2004).

In Egypt, Zygophyllum album is an omnipresent species with a wider ecological range than Zygophyllum coccineum (Kassas and Girgis, 1965). It was recognized in several habitats of the country, such as in the littoral salt marshes (Kassas and Zahran, 1967), in the inland deserts, in the wadis of the limestone country (Kassas and Girgis, 1964), in the sand dunes of the oases of the Western Desert (Zahran, 1972), and in the inland salt marshes of Wadi El Natrun (Zahran and Girgis, 1970). The soil supporting its growth is characterized by high contents of sand, salinity, chlorides, sodium, and sulfates. This result is similar to those of all other relevant studies (Migahid et al., 1996; Hussein, 2005). Several authors recognized this group, including Kassas and Girgis (1965) in some wadis of the limestone desert extending to the east of the Nile Valley, Ayyad and El-Ghareeb (1982) in salt marshes of the western Mediterranean desert of Egypt, Shaltout and El-Sheikh (2002) in demolished houses and abandoned fields and along the terraces of railways on the borders of the Nile Delta, and Abd El-Ghani and El-Sawaf (2005) in the saline depressions between El Arish and

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Rafah on northeastern Mediterranean coast of the Sinai. In the salt marsh stands of the Nile, the soluble chlorides in the soil of *Z. album* were at higher levels than the sulfates. This was also reported by Kassas and Zahran (1967), who concluded that in the soil of *Z. album* the levels of chlorides nearly equal or are higher than those of sulfates.

With regards to the phytogeographical territories, the Sinai Peninsula and the Mediterranean regions were home to most of the succulent species. The vegetation associated with the 5 most common succulent plants in the arid lands of Egypt was analyzed, and variations in their floristic composition were described. Altogether, 137 species belonging to 37 families of vascular plants were recorded in this study. The most succulent species-rich families were Chenopodiaceae, Aizoaceae, Zygophyllaceae, and Crassulaceae. TWINSPAN classification revealed 8 vegetation groups; most of the studied succulent plants were assigned to a certain group. Vegetation associated with Arthrocnemum macrostachyum was affected by Mg and EC; Zygophyllum album was affected by SO..., EC, and Ca++; and Anabasis articulata, Haloxylon salicornicum, and Zygophyllum coccineum were highly affected by percentages of sand and clay and values of pH, CaCO₃, and N.

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Appendix. Distribution of succulent flora in the different phytogeographic regions of Egypt. N = Nile	region, M = Mediterranean
region, O = Oases, D = All deserts except Sinai, R = Red Sea, GE = Gebel Elba, S = Sinai Peninsula. Sou	rces: B = Boulos (1999, 2000,
2002; 2005), T = Täckholm (1974), E = El Hadidi and Fayed (1994/95).	

Families	Species	Habit	Ν	0	М	D	R	GE	S
1) Succulent leaf									
Aizoaceae	Aizoon canariense	Ann. herb			B TE	B TE		B T	B TE
Aizoaceae	Aizoon hispanicum	Ann. herb	B T		B TE	B TE			B TE
Aizoaceae	Mesembryanthemum crystallinum	Ann. herb	B T		B TE	B TE			В
Aizoaceae	Mesembryanthemum forsskaolii	Ann. herb		B TE	B TE	B TE			B TE
Aizoaceae	Mesembryanthemum nodiflorum	Ann. herb	B T		B TE				В
Aizoaceae	Sesuvium sesuvioides	Ann. herb						B TE	
Aizoaceae	Trianthema portulacastrum	Ann. herb				_	_	B TE	
Aizoaceae	Trianthema triquetra	Ann. herb				B TE	B TE	B TE	
Aizoaceae	Zaleya decandra	Ann. herb	_			_	_	B TE	_
Aizoaceae	Zaleya pentandra	Ann. herb	B TE		_	B TE	B TE	B TE	B TE
Caryophyllaceae	Polycarpon succulentum	Ann. herb	B T		B TE	B TE	_	-	B TE
Caryophyllaceae	Sclerocephalus arabicus	Ann. herb				B TE	B TE	B TE	B TE
Chenopodiaceae	Halocnemum strobilaceum	Shrub	B TE		B TE	B TE	B TE		B TE
Chenopodiaceae	Halopeplis amplexicaulis	Shrub	B T	B TE	B TE		_		В
Chenopodiaceae	Halopeplis perfoliata	Shrub			B TE		B TE		В
Chenopodiaceae	Salsola imbricata subsp. gaetula	Shrub		B E	B E	B E			В
Chenopodiaceae	Salsola imbricata subsp. imbricata	Shrub	В	B TE	P	B TE		B TE	B T
Chenopodiaceae	Salsola kali	Ann. herb	B T	D	B TE P	Т			B T P
Chenopodiaceae	Salsola tetrandra	Shrub	P	B T	B TE P	B TE P			B TE P
Chenopodiaceae	Salsola volkensii	Ann. herb	B T		B TE	B TE P			B E D
Chenopodiaceae	Seidlitzia rosmarinus	Shrub				B TE P	n	P	B TE
Chenopodiaceae	Sevada schimperi	Shrub	P	D	D	B TE P	B TE	B TE	
Chenopodiaceae	Suaeda aegyptiaca	Ann. herb	B T	B TE	B TE P	B TE			В
Chenopodiaceae	Suaeda altissima	Ann. herb		Ð	B TE				
Chenopodiaceae	Suaeda maritima	Ann. herb	B T	B E	B TE	B TE			

Appendix. (continued).

Chenopodiaceae	Suaeda monoica	Shrub		B TE		B T	B TE	B T	B T
Chenopodiaceae	Suaeda palaestina	Shrub			B E				В
Chenopodiaceae	Suaeda pruinosa	Shrub			B TE	TE			В
Chenopodiaceae	Suaeda splendens	Ann. herb	B T		B TE	Е			В
Chenopodiaceae	Suaeda vera	Shrub	B T		B TE	B T	Т	Т	B T
Chenopodiaceae	Suaeda vermiculata	Shrub	B T	B T	B TE	B TE	B TE		B TE
Chenopodiaceae	Traganum nudatum	Shrub		B T	B E	B TE			B T
Commelinaceae	Commelina forsskoalii	Per. herb						В	
Commelinaceae	Cyanotis barbata	Per.						B TE	
Asteraceae	Limbarda crithmoides	Shrub	B TE	B TE	B TE				
Crassulaceae	Crassula alata	Ann. herb	Т		B TE				
Crassulaceae	Rosularia lineata	Per. herb				TE			В
Crassulaceae	Umbilicus botryoides	Per. herb						B TE	
Crassulaceae	Umbilicus horizontalis var. horizontalis	Per. herb			B TE				В
Crassulaceae	Umbilicus rupestris	Per. herb							B TE
Cruciferae	Cakile maritima subsp. aegyptiaca	Ann. herb	B T		B TE	Т			В
Cruciferae	Moricandia sinaica	Per. herb				B T			B TE
Peganaceae	Tetradiclis tenella	Ann. herb			B TE				
Portulaceae	Portulaca oleracea subsp. stellata	Ann. herb	TE	Т	Т	Е			B T
Portulaceae	Portulaca oleracea subsp. nitida	Ann. herb	B TE	B TE	B TE	B E			B T
Portulaceae	Portulaca oleracea subsp. oleracea	Ann. herb	B TE	Т	TE			B E	Т
Solanaceae	Hyoscyamus boveanus	Per. herb	В	B TE		B TE	B TE		B TE
Solanaceae	Hyoscyamus muticus	Per. herb	B T	B TE	B TE	B TE	B TE	B E	B TE
Famaricaceae	Reaumuria hirtella var. brachylepis	Shrub			TE	TE			B E
Famaricaceae	Reaumuria hirtella var. hirtella	Shrub			B TE	B TE			B TE
Famaricaceae	Reaumuria hirtella var. palaestina	Shrub			E	TE			B TE
Tamaricaceae	Reaumuria negevensis	Shrub				TE			В
Tamaricaceae	Reaumuria vermiculata	Shrub		B TE	B TE	B TE			В
Zygophyllaceae	Fagonia arabica var. viscidissima	Shrub		B TE	Е	B TE	Е		

Appendix. (continued).

Zygophyllaceae	Zygophyllum aegyptium	Shrub	В		B E	Б			B
Zygophyllaceae	Zygophyllum album	Shrub		B	В	E B TT	B		E B
Zygophyllaceae	Zygophyllum coccineum	Shrub		TE B TE	TE	TE B TE	TE B TE		TE B E
Zygophyllaceae	Zygophyllum dumosum	Shrub		ΙL		B TE	ΙĽ		E B TE
Zygophyllaceae	Zygophyllum simplex	Ann. herb				B TE	B TE	B TE	B T
2) Succulent stem						1L	1L	1L	1
Asclepiadaceae	Caralluma acutangula	Per. herb						B T	
Asclepiadaceae	Caralluma edulis	Per. herb						B T	
Asclepiadaceae	Caralluma europaea	Per. herb			B TE			1	В
Asclepiadaceae	Caralluma sinaica	Per. herb			1L	TE			B TE
Chenopodiaceae	Anabasis articulate	Shrub		B TE	B TE	B TE	Е		B TE
Chenopodiaceae	Anabasis setifera	Shrub		1L	1L	B TE	B T	B T	B TE
Chenopodiaceae	Arthrocnemum macrostachyum	Shrub	B T	B TE	B TE	B TE	B TE	E	B T
Chenopodiaceae	Haloxylon negevensis	Shrub	1	1L	11	1L	1L		В
Chenopodiaceae	Haloxylon salicornicum	Shrub		B TE	B TE	B TE	B TE		B TE
Chenopodiaceae	Salicornia europaea	Ann. herb	B TE	B T	B TE	1L	1L		B
Chenopodiaceae	Sarcocornia fruticosa	Shrub	B T	B TE	B TE	B TE			В
Chenopodiaceae	Sarcocornia perennis	Shrub	E	12	B TE	Т			В
Elatinaceae	Bergia capensis	Ann. herb	B TE	B TE	12	-			
Euphorbiaceae	Euphorbia consobrina	Shrub	12	12			B T	B T	
Euphorbiaceae	Euphorbia mauritanica	Shrub	B T		B T		_	-	
Euphorbiaceae	Euphorbia polyacantha	Shrub						B T	
Orobanchaceae	Cistanche phelypaea	Per. herb	B T	B TE	B TE	B TE	B TE	-	B TE
Orobanchaceae	Cistanche sala	Per. herb	-	12	12	E	12		В
Orobanchaceae	Cistanche tubulosa var. albiflora	Per. herb							B T
Orobanchaceae	Cistanche tubulosa var. tubulosa	Per. herb	TE		B T	B TE		B TE	B TE
Orobanchaceae	Orobanche crenata	Ann. herb	B TE	TE	B TE	B TE			B TE
Sphenocleaceae	Sphenoclea zeylanica	Ann. herb	TE	B TE	T	11			11
Vitaceae	Cissus quadrangularis	Per. herb	11	11	ī			B TE	