Plant Ecology and Evolution 151 (2): 175–184, 2018
https://doi.org/10.5091/plecevo.2018.1370

REGULAR PAPER

Edaphic characterization of coastal Western Mediterranean *Limonium* (Plumbaginaceae)

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Introduction – Edaphic factors influence the structure and composition of plant communities. The main objective is to identify soil properties associated with the presence of different *Limonium* species.
Methods – We conducted a systematic phytocoenological and edaphic survey over 37 locations across the Balearic archipelago. Canonical Correspondence Analysis was applied to the physicochemical characteristics of soils in which 29 species of *Limonium* grow.
Results – The distribution of *Limonium* species has a high correlation to specific edaphic factors. The species can be clustered into four major groups. The first group represents species with a high edaphic selectivity – soils characterized by having a high proportion of sand, SO_4^{2-} and Ca^{2+}. The second group is composed of species with high levels of SAR, OM and SO_4^{2-} /Cl^- ratio. The third group includes species present in soils with a loamy texture, low Ca^{2+} /Mg^{2+} ratio and high levels of CO_3^{2-} and Mg^{2+}. The fourth group includes plants which colonize soils that have a sandy texture, low salinity and high proportion of CO_3^{2-}.
Conclusions – A strong correlation between the distribution of *Limonium* species and soil characteristics exist. The study contributes to the establishment of foundations for habitat conservation, cultivation and recovery projects for endangered species of *Limonium*.

Key words – *Limonium*, soil characterization, sulphates, saline habitats, conservation.

INTRODUCTION

Spatio-temporal gradients of soil salinity and water determine zonation and distribution of plant taxa of coastal vegetation, and habitats of salt marsh and endoreic basins (Chapman 1974, Álvarez-Rogel et al. 2000, St. Omer 2004). In addition, topography determines distribution of levels salt concentration and, accordingly, plant zoning in these areas (Chapman 1976, van Wijnen et al. 1997, Bockelmann et al. 2002), particularly in Mediterranean ecosystems (Álvarez-Rogel et al. 2001, Costa et al. 2003, Acosta et al. 2007).

In forests and other landscapes, the successive stages of colonization (like soil evolution) allow the incorporation of new species that replace the original vegetation. Succession of species defines a vegetation series that leads to a final stable community – climax vegetation – with higher levels of resource optimization (Clements 1916, Braun-Blanquet 1964, Odum 1983). This proposed scheme of dynamic vegetation is consistent when limiting factors of plant development are linked to climatic conditions (climatophilous vegetation). However, over long periods of time, in salt marshes and saline habitats in general, the vegetation succession, as in other types of edaphic vegetation (as sand dunes, aquatic and marsh vegetation), does not always follow the climatic pattern, since the succession is preferably linked to the physical-chemical characteristics of soil (Redfield 1972, Beeftink 1977, Adam 1990).

The definition of halophile plants as taxa that can tolerate up to 200 mM NaCl (Flowers & Colmer 2008) is applied to most species colonizing salt marshes where NaCl from sea water is the principal salt component. Moreover, intertidal periods induce variations in water levels, which can even reach dryness. The life cycle of halophytes is generally linked to a progressive limitation of plant development derived from physiological limitations. Among other effects, salinity causes a reduction in growth parameters (Naqvi et al. 1997), a decrease in potassium absorption (Girija et al. 2002), stomatal conductance or CO_2 assimilation (Fernán-

ISSN: 2032-3913 (print) – 2032-3921 (online)

dez-García et al. 2004). For that reason, the link between the presence of halophytes and microtopographic relief may be explained by considering, when evaporation periods are long, that salts concentration in surface soils may become very high in depressions (Adam 1990).

Major coastal gypsum substrates in the Balearics are anthropogenic. For more than 25 centuries, some areas of the coastal wetlands have been exploited for the extraction of salt (Vilà 1953, 2000). Sulphates, precipitated during the NaCl crystallization process, have been extracted from the plots (evaporators) periodically to avoid clogging and to facilitate the industrial process. Therefore, an artificial substrate with a high proportion of sulphates has accumulated in the areas surrounding the deposits. Unlike other Western Mediterranean halophyte species (Álvarez-Rogel et al. 2001, Baumberger et al. 2012b), the soils of the *Limonium* populations studied are not subject to seasonal flooding. *Limonium* sp. populations grow on slight elevations of soil within areas of vegetation occupied by other types of halophytic vegetation (*Sarcocornia* sp., *Arthrocnemum macrostachyum* (Moric.) K.Koch, *Suaeda vera* Forssk. ex J.F.Gmel., etc.).

Species of the genus *Limonium* Mill. are established in the more saline areas of the marshes and are usually exposed to longer drought periods compared to other communities of halophilous genera (*Arthrocnemum* Moq., *Sarcocornia* A.J.Scott or *Suaeda* Forssk. ex J.F.Gmel.). The presence of *Limonium* species normally indicates a limit of colonization by other halophilous species in terms of salt quantity, quality and water deficit.

Communities of *Limonium* sp. (Ord. *Limonietalia* Br.- Bl. et O. Bolòs 1957) have been reported (Bolòs 1967, Castroviejo & Cirujano 1980, Llorens 1986) to establish ecological differences from neighbouring halophyte succulent communities (*Arthrocnemum*, *Salicornia* sp. etc.; Ord. *Arthrocnemetalia fruticosa* Br.-Bl. 1931) which have higher moisture requirements. Slight elevations of soil or longer periods of dryness allow colonization by different species of *Limonium*, creating associated sequences of communities.

Moreover, in some studies on halophilous vegetation of the Western Mediterranean, greater tolerance or adaptation of some species to saline soils with high concentration of sulphates was detected – e.g. for *L. girardianum* (Guss.) Fourr., *L. angustibracteatum* Erben (Costa & Boira 1981) or *L. echioides* (L.) Mill. (Boira et al. 2002). Studies of *Limonium* on the coastal rocks and salt marshes of the Balearic Islands have indicated that the distribution of endemic species is strongly correlated to the chemical characteristics of soils (Llorens 1985a, 1986). Long periods of dryness and high proportions of sulphates and carbonates constitute the principal determinant factors of selective colonization of the species.

The genus *Limonium* comprises many hemicryptophytes (perennial herbs and subshrubs) with a world-wide distribution in arid environments, coastal marshes and cliffs, saline alluvial soils and gypseous steppes. A very high percentage of *Limonium* diversity is centred in the Mediterranean basin (Erben 1993). The Western Mediterranean basin is one of the main centres of origin and dissemination of the genus and possesses a high plant diversity (Bolòs 1967, Pignatti 1982, Greuter et al. 1989, Erben 1993, Pavon 2005), with nearly 300 taxa (Llorens 1986, Erben 1993, Palacios et al. 2000, Sáez 2005), mostly endangered, endemic or rare. In the Balearic Islands 53 species of them are present.

The diversity of flora and habitats present in the Balearic archipelago determines its appeal as a model territory for the study of the ecology of the species of this genus.

The current existence of many taxa is related to frequent hybridization that results in a high proportion of polyploids (Erben 1993, Castro & Rosselló 2007). Consequently, many *Limonium* species depend on agamospermous reproduction. This reproductive feature limits their ability to adapt to a changing environment through genetic recombinations (Erben 1979, Cowan et al. 1998, Atelari & Georgiou 1999, 2002, Baumberger et al. 2012a). Apomictic reproduction is common in many species of *Limonium* in the Mediterranean (Brullo & Erben 2016). Accordingly, in the Balearic Islands, the greatest number of species is apomictic. This is supported by the apomictic dominant karyotypes (2n+1), where the plant can produce viable seeds without fertilization. This increases its dispersion potential, allowing the colonization of special habitats with particular climatic or edaphic stress (table 1), as it is not dependent on the availability of pollination vectors. This is why many species have outstanding adaptations to very specific soil conditions, presenting fragmented populations over long distances (Baumberger et al. 2012b).

In this paper, phytocoenological and ecological characteristics of various, mostly endemic, species of *Limonium* found in the Balearic archipelago have been studied. The aims of the present study were: (1) to investigate phytocoenological characteristics of the *Limonium* populations studied; (2) to determine the relation of the main communities to physical/chemical properties of soils; and (3) to discuss the genetic and biological characteristics of the species of *Limonium* in relation to their adaptive capacity in different types of saline soils – mainly the physical/chemical characteristics and relative proportion of anions and cations.

MATERIAL AND METHODS

Study species and sites

The study was carried out in the coastal areas of the islands of Majorca, Ibiza and Formentera (fig. 1). General background information was provided by floristic, chorological and genetic studies of the flora and vegetation of the salt marshes and coasts of these islands (Llorens 1985a, 1985b, 1986, Llorens & Tébar 1988, Erben 1989, 1993, Castro & Rosselló 2007).

The climate is typically Mediterranean, with mild temperatures (average annual between 16.5 and 18.1ºC) and irregular rainfall (average annual between 340 and 680 mm), occurring primarily in autumn and spring. The summers are hot and dry. From a bioclimatic viewpoint, the areas of Formentera, Ibiza and southern Majorca are included in the Thermo-Mediterranean semiarid inferior belt; and the northern Majorca zone in the Thermo-Mediterranean subhumid inferior belt (Rivas-Martínez 1984).

Table 1 – References of karyotypes, reproduction and original habitat of *Limonium* species.
CR, chromosome number. (*). D, diploid; Tr, triploid; Te, tetraploid; He, hexaploid; A, aneuploid; APO, apomictic rep.; SEX, sexual rep. H, habitat; (**) RC, Rocky coastline; DSM, coastal dunes and salt marsh; CS, coastal slopes; BS, brackish soils. GD, geographical distribution; IBZ, Ibiza; FOR, Formentera; MA, Majorca; MI, Minorca; MED, Mediterranean; W MED, Western Mediterranean. Nomenclature of sampling locations according to Figure 1.

Species	CR	Polyploidy (*)			H (**)	GD	Sampling locations
L. algarvense Erben	25	3x	2(8)+9 A	APO	RC/DSM	W MED	10
L. alcudianum Erben	26–27	3x	3x9 Tr 2(9)+8 A	APO	DSM	MA	11, 12
L. antonii-llorensii L.Llorens	27	3x	3x9 Tr	APO	DSM	MA	22, 23
L. balearicum (Pignatti) Brullo	27	3x	3x9 Tr	APO	RC/CS	MA	13, 14
L. barceloi Gil & L.Llorens	36	4x	4(9) Te	APO	DSM	MA	28
L. biflorum (Pignatti) Pignatti	25	3x	2(8)+9 A	APO	RC/BS	MA, ME	15, 18
L. boirae L.Llorens & Tébar	35	4x	3(9)+8 A	APO	DSM/BS	MA	32
L. camposanum Erben	26–27	3x	3x9 Tr 2(9)+8 A	APO	RC/DSM	MA	22
L. carregadorense Erben	27	3x	3x9 Tr	APO	RC/CS	MA	16
L. companyonis (Gren. & Billot) Kuntze	27	3x	3x9 Tr 2(9)+8 A	APO	RC/DSM	W MED	3, 11, 20, 23, 29, 37
L. echioides (L.) Mill.	18	2x	2(9) D	SEX	RC/DSM	MED	3, 6; 17, 27, 34
L. ejulabilis Rosselló Mus & Soler	24–25	3x	3x8 Tr 2(8)+9 A	APO	DSM	MA	34
L. escarrei L.Llorens	27	3x	3x9 Tr	APO	RC/CS	MA	14
L. formenterae L.Llorens	25	3x	2(8)+9 A	APO	DSM	EIV, FOR	2, 3, 5
L. gibertii (Sennen) Sennen	26–27	3x	3x9 Tr 2(9)+8A	APO	RC	W MED	29, 30, 31, 33
L. grosii L.Llorens	36	4x	4(9) Te	APO	DSM	FOR	3, 4
L. gymnesicum Erben	27	3x	3(9) Tr	APO	RC	MA	13, 19
L. heterospicatum Erben	26	3x	3(9) Tr	APO	DSM	EIV, FOR	2, 5, 7, 8, 9
L. magallufianum L.Llorens	26	3x	2(9)+8 A	APO	DSM	MA	32
L. majoricum Pignatti	27	3x	3(9) Tr	APO	RC	MA	13
L. marisolii L.Llorens	25–27–54	3x–6x	3(9) Tr 9+2(8) A 6(9) He	APO	RC/CS	MA	25, 26
L. migjornense L.Llorens	25–50	3x–6x	2(8)+9 A 4(8)+2(9) A	APO	DSM	MA	22
L. minutum (L.) Chaz.	18	2x–3x	2(9) D 3x9Tr	SEX APO	RC/CS	EIV, FOR, MA	1, 15, 20, 21, 24, 26, 35
L. pseudodictyocladum (Pignatti) L.Llorens	18	2x	2(9) D	SEX	RC/CS	MA	16
L. retusum L.Llorens	25	3x	2(8)+9 A	APO	DSM	FOR	2, 3, 5
L. tamarindanum Erben	27	3x	3(9) Tr	APO	RC/DSM	MA, ME	20
L. validum Erben	27	3x	3x9 Tr	APO	DSM	MA	32, 34, 35, 36
L. virgatum (Willd.) Fourr.	27–36	3x–4x	3x9 Tr 4(9) Te	APO	RC/DSM	MED	11, 21, 30, 32, 20, 23, 12, 36, 24
L. wiedmannii Erben	24	3x	3x8 Tr	APO	DSM	FOR	1, 5

The natural landscape is mostly dominated by coastal, calcareous rocks aligned horizontally and salt marshes behind the coastal line. Maritime cliffs are Quaternary eolianites (eolian calcarenites) – marine sediments formed by carbonate cementation including skeletal grains of coralline algae, molluscs and foraminifera (Tortonian stage, Upper Miocene, 11.6 ma). They are predominant in the Balearic Islands but especially in Majorca (Fornós 2011). More than 50% of these coastal formations can be made up of carbonated elements which constitute a special niche for plant colonization.

Some salt marsh zones occupy depressions between the succession of wide dune ridges parallel to the coastline and adjacent to the subsiding basins (e.g. Salines of Formentera, Ibiza and s'Avall, SE Majorca). Periodic flooding – natural or artificial – by sea water, give them edaphic characteristics with variable soil texture and high concentrations of chlorides and sulphates. The selection of sites included dunes, sea cliffs, salt marshes and zones next to industrial salt extraction areas (including those in which bargain materials obtained from salt extraction are deposited) and was based on the presence of *Limonium* species regardless of any floristic accompaniment. Like previous research of *Limonium* ecology (Boorman 1971), the study of other species of the early communities of the salt marsh succession has been excluded.

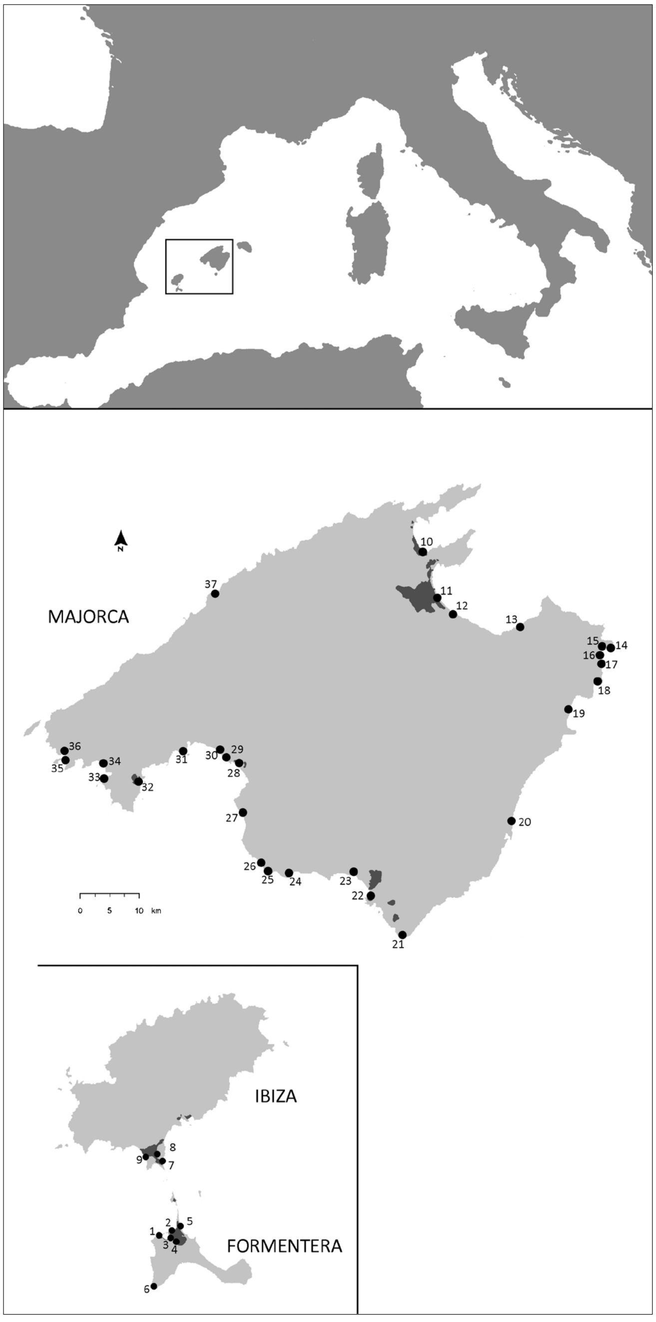

Figure 1 – Sampling locations. Formentera: 1, Pedreres; 2, Salines Ferrer; 3, Estanyets; 4, Brolls; 5, Salines Marroig; 6, Cap Berberia. Ibiza: 7, Estanys; 8, Sa Canal; 9, Codolar. Majorca: 10, Albufereta; 11, Alcudia; 12, Can Picafort; 13, Colònia St. Pere; 14, Punta de cala Gat; 15, Cala Gat; 16, Carregador Capdepera; 17, Cala Provençal; 18, Canyamel; 19, Port Vell; 20, Cala Murada; 21, Cap Salines; 22, Salines s'Avall; 23, Salines Palmer; 24, Sa Ràpita; 25, Cala Beltran; 26, Pas Senyora; 27, Pedreres Seu; 28, Fontanelles; 29, Carnatge; 30, Coll d'en Rabassa; 31, Porto Pi; 32, Magaluf; 33, Santa Ponça; 34, Costa Calma; 35, Camp de Mar; 36, Port Andratx; 37, Sóller.

A total of 29 species (table 1, electronic appendix), from 37 representative locations, were studied – 24 are endemic to the Balearic Islands, three have a Western Mediterranean distribution and two are occurring throughout the Mediterranean (table 1).

Methods

A total of 68 inventories, carried out on surfaces of 2 m^2, were collected according to the phytosociological methodology (Braun-Blanquet 1964).

To relate edaphic variables to *Limonium* species, soil samples were taken for each vegetation inventory. The depth of soil samples (10–20 cm) was determined by the extent of the roots (rhizosphere level). Before laboratory analysis, the samples were air-dried and screened through a 2 mm sieve to remove coarse fraction.

Soil texture was analysed following Robinson's pipette method, after previous dispersion with sodium hexametaphosphate (Rzasa & Owczarzak 2013). Bernard's calcimeter method was applied for total calcium carbonate (UNE 7-367), which estimates the volume of carbon dioxide (CO_2) generated by the sample after digestion with hydrochloric acid versus volume of carbon dioxide (CO_2) (Nelson & Sommers 1996). Soil pH was determined in aqueous suspension 1:1 (Soil Survey Staff 2014). For the measurement of the potential pH (KCl pH) a sample of 10 g of soil dissolved in 25 ml of a 0.1 N KCl solution was used (Chapman & Pratt 1961). Electrical conductivity of the saturation extract was determined by a Hanna conductivity meter; the results, at 25ºC, are given in mS cm^{-1}. From this aqueous solution, water soluble Ca^{2+}, Mg^{2+}, Na^{+} and K^{+} levels were determined using an atomic absorption spectrophotometer (Perkin-Elmer 2380). A standard method of determining gypsum in soils was applied – sulphate was dissolved from the soil samples by extracting the soil and then dissolving it with successively greater water/soil ratios until all the sulphate was dissolved in the extract. Total sulphate was measured by gravimetry (Soil Survey Staff 2014), chlorides by precipitation of silver chloride (Mohr's method) and sodium absorption ratio (SAR) according to Richard's equation (Richards 1954). Organic matter was measured by oxidation with a potassium dichromate ($K_2Cr_2O_7$)-sulfuric acid mixture (Walkley & Black 1934).

Statistical data processing

Phytocoenological groups, based on floristic distances, was carried out by application of the TWINSPAN method (PC-ORD. ver. 6.; McCune & Mefford 2011).

To elucidate the relationships between plant species, phytocoenological groups and spatial changes in edaphic variables, Canonical Correspondence Analysis – CCA – (ter Braak 1987) was performed using the PC- ORD. ver. 6 software. The mean discrimination of edaphic values for the phytocoenological groups is based in the minimum significant difference method (LSD, Fisher; $P \leq 0.05$). The triplot diagrams – presented according to total variance – show the

Table 2 – **Canonical Correspondence Analysis.**
Axis summary statistics (3 canonical axes extracted).

	Axis 1	Axis 2	Axis 3
Eigenvalue	0.989	0.908	0.892
Cumulative % variance explained	4.6	8.7	12.8
Pearson Correlation (Spp - Environmental)	0.996	0.971	0.98

patterns of variation in the community composition best fitted to the environmental variables, although species performance may be influenced by soil conditions related to or associated with these variables.

Previous to ANOVA analysis (StatgraphicsPlus ver. 5.1 2001), the Shapiro-Wilk normality test was used. Analysis for homoscedasticity of variances, after data transformation ($\sqrt{x}$) for the variables that were not following the normal distribution, was carried out by the Cochran and Levene tests.

RESULTS

Phytocoenological groups

In the studied cases, both the standardized skewness and kurtosis values were within the range expected for data from a normal distribution.

Following the matrix TWINSPAN analysis results of 68 vegetation samples, four associations were established considering species frequency (electronic appendix).

The first group (G1) comprises four island microendemics especially from Formentera. *Limonium heterospicatum* is also located in Ibiza, where it appears in three monospecific plots (Invs. 13, 14 and 15, electronic appendix). In Formentera, where the association is genuinely represented, it appears combined with other three characteristic species: *L. formenterae*, *L. retusum* and *L wiedmannii*. In general, the populations are quite dense with the highest degrees of coverage arriving to 50%, in Marroig, Formentera.

Species in the second group (G2, electronic appendix) show a low degree of sociability. This is the characteristic that does not allow the inclusion of the paradoxical association in other groups. However, they have common ecological features. This community appears in a wide range of habitats, like salt marshes, coastal dunes and rocky areas on the island of Majorca.

Limonium camposanum, *L. antonii-llorensii* and *L. migjornense* (G3) are three microendemics distributed in salt marshes and brackish soils behind the littoral dunes of Colònia St. Jordi and Salines de s'Avall. The four inventories that allow us to define this association (electronic appendix) include isolated species or species combined with other of sporadically present species, or species with wider chorological and ecological spectrum (*L. virgatum*).

The last group (G4) includes species with a major ecological and biogeographical spectrum (W Mediterranean and general Balearic endemics). Floristic distances determine lower rates of correlation between vegetation samples; some of them with a single species uncorrelated to the rest (*L. alcudianum*, electronic appendix, invs. 24 and 66).

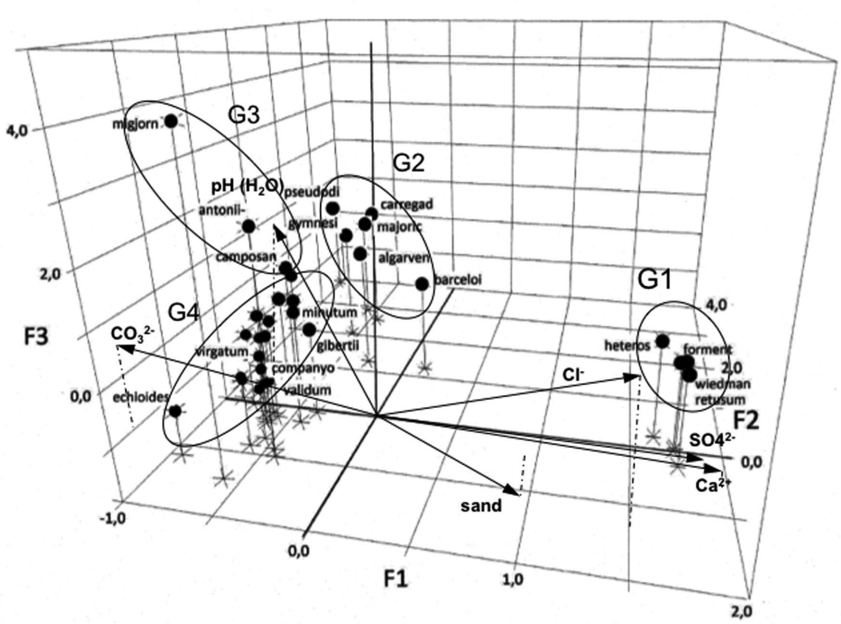

Figure 2 – CCA joint triplot of phytocoenological groups (G1, G2, G3 and G4), characteristics species (acronym), and relationships to the edaphic variables (vectors).

Environmental relationships, ecological gradients of edaphic variables

After using the CCA of the species and soil data inventories, the three first factors extracted only explained 18.85% of the variance. The ordering of species according to the Euclidean distances permitted to characterize the four groups.

The relationship of both taxa and sociological groups to the edaphic variables, extracted from the application of CCA, allowed us to establish the distribution of the species and emerging groups through a species-environment triplot (table 2, fig. 2).

The edaphic variables explaining most of the floristic are sorted in the following order (fig. 2) – sulphates, Cl^-, Ca^{2+}, salinity (Cond. mS/cm) and sandy texture – and had a strong correlation to the positive values of Axis 1. Moreover, carbonates, magnesium and pH (H2O) were related to the negatives values of Axis 1 and Axis 2, and the positive values of Axis 3.

The species linked to the positive values of Axis 1 (G1) are endemics of Formentera, constituting fragmented populations in the sandy soils and salt marshes (*L. formenterae*, *L. retusum*, *L. heterospicatum* and *L. wiedmannii*), as well as of Ibiza (*L. heterospicatum*) (table 3). These species constitute a phytocoenological group with a strong correlation to the positive gradient of sand (81.5%), sulphates (49.2 SO_4^{2-} meq/l), chlorides (4.2 Cl^- meq/l) and calcium (121.6 Ca^{2+} meq/100 g). The soils from these species also show high values of Ca^{2+}/Mg^{2+} (table 3).

The G2 group comprises populations of the sandy soil salt marsh or rocky coast line. It is composed of endemics of Majorca, like *L. barceloi*, *L. majoricum*, *L. gymnesicum*, *L. carregadorense*, *L. pseudodictyocladum*, and *L. algarvense*; this last one is not endemic but has a wide distribution (W Mediterranean). Although they show intermediate differential values with major heterogeneity of factors such as soil texture, sulphates and total carbonates compared to other groups (table 3), the probability of presence is related to the highest values of SAR (0.5), MO (6.87%) and SO_4^{2-}/Cl^- ratio (3.4) (table 3).

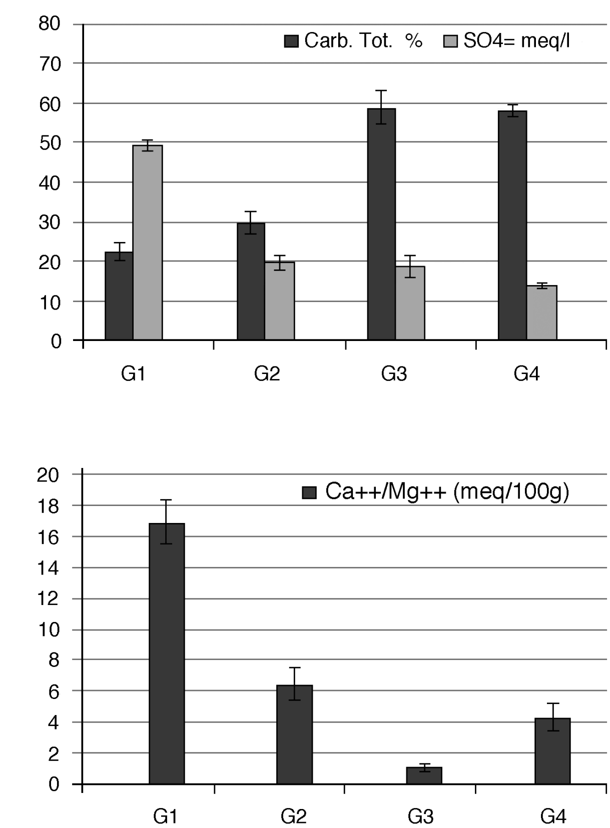

Figure 3 – Differential values of three edaphic variables for the four *Limonium* ecotypes.

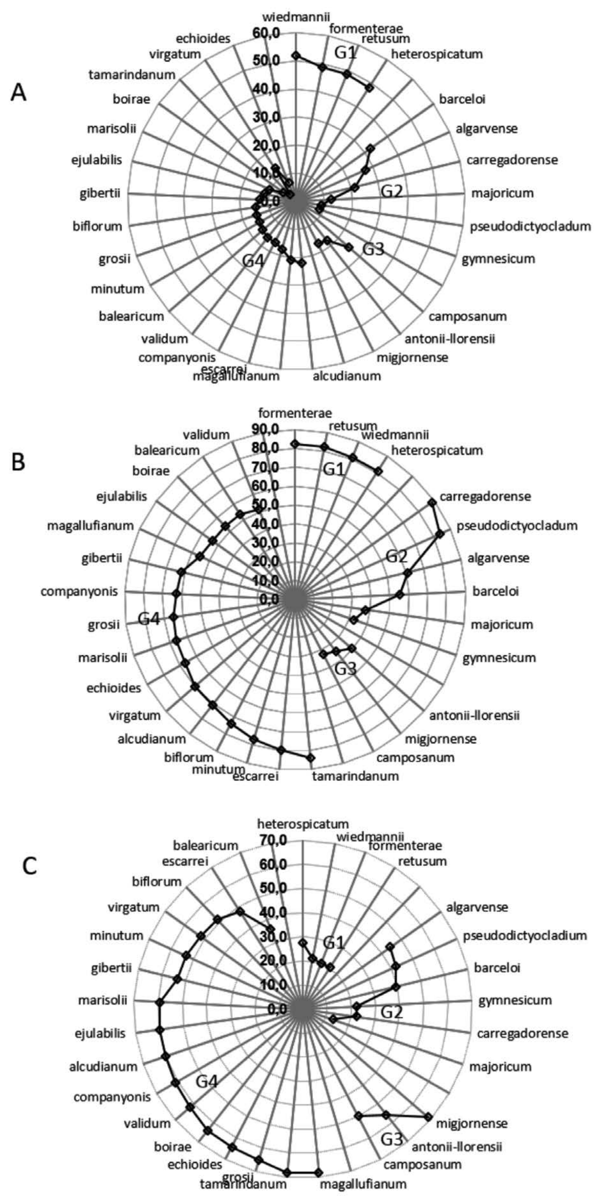

Figure 4 – Gradation of differential edaphic variables (mean values) for the four ecotypes (G1, G2, G3 and G4) of *Limonium* spp. A: sulphates (SO_4^{2-} meq/l); B: sand (%); C: carbonates (CO_3^{2-} %).

Table 3 – Significant differential values of soil analysis.
x̄: mean; s.e.: standard error; Ec: Ecotypes; O.M.: organic matter; Cond.: conductivity; SAR: sodium; values followed by the same superscript letter within the same column are not significantly differences. Range Tests (95.0%, LSD –Least Significant Differences).

		Sand %			Clay %			Loam %			O.M. %			H_2O pH			KCl pH		
Ec	n	x̄	s.e.		x̄	s.e.		x̄	s.e.		x̄	s.e.		x̄	s.e.		x̄	s.e.	
G1	22	**81.5**	2.44	a	8.75	1.37	a	9.77	1.3	a	6.4	0.27	ab	**8.22**	0.04	a	8	0.04	a
G2	12	53.1	3.30	b	22.53	1.86	b	24.3	1.8	b	6.9	0.37	a	8.49	0.06	bc	8.2	0.05	b
G3	6	36.5	4.66	c	24.85	2.63	b	38.6	2.6	c	5.2	0.53	bc	8.66	0.08	d	8.4	0.07	c
G4	62	65.2	1.45	d	16.91	0.82	c	18.3	0.8	d	5.3	0.16	c	8.4	0.03	c	8.1	0.02	b

		Cond. mS/cm			Carb. Tot. %			SO_4^{2-} meq/l			Cl^- meq/l			Ca^{2+} (meq/100g)			Mg^{2+} (meq/100g)		
Ec	n	x̄	s.e.		x̄	s.e.		x̄	s.e.		x̄	s.e.		x̄	s.e.		x̄	s.e.	
G1	22	**6.8**	0.29	a	22.5	2.10	a	**49.2**	1.45	a	**40.2**	2.01	a	**121.586**	1.91	a	7.2	0.95	a
G2	12	2.2	0.39	b	29.7	2.85	b	19.7	1.96	b	12.0	2.72	b	26.4	2.59	b	4.1	1.29	a
G3	6	**4.3**	0.55	c	**59.0**	4.02	c	18.7	2.77	cb	23.9	3.85	c	27.7	3.66	b	**25.8**	1.83	b
G4	62	2.1	0.17	b	**58.2**	1.25	c	13.9	0.86	cb	13.8	1.20	b	26.2	1.14	b	6.1	0.57	a

		Na^+ (meq/100g)			K^+ (meq/100g)			Ca^{2+}/Mg^{2+}			SO_4^{2-}/Cl^-			SAR		
Ec	n	x̄	s.e.		x̄	s.e.		x̄	s.e.		x̄	s.e.		x̄	s.e.	
G1	22	21.5	1.60	a	2.1	0.26	a	**18.81**	0.94	a	1.3	0.5	a	0.2	0.04	a
G2	12	16.4	2.16	b	2.4	0.36	a	8.3	1.27	b	**3.4**	0.7	b	**0.5**	0.06	b
G3	6	17.3	3.06	ab	1.5	0.51	ab	1.9	1.79	c	0.8	1.0	a	0.3	0.08	abc
G4	62	11.6	0.95	b	1.4	0.15	b	5.5	0.55	b	1.8	0.3	a	0.4	0.02	c

Species included in the G3 and G4 groups grow in soils with a higher differential proportion of carbonates (95%, LSD intervals). From groups G1 to G4 there is a positive trend of an increase in the proportion of the carbonates and a decrease in sulphates (fig. 3A).

The third group (G3) includes *L. camposanum*, *L. antonii-llorensii* and *L. migjornense*, endemic species characteristic of the saline coastal soils on calcareous dolomites on the E and S coastline of the island of Majorca. Presence of these species strongly corresponds to the positive values of Axis 3. Soils tend to have a loamy texture with a high proportion of carbonates (59.0%). Compared to other communities, a high concentration of Mg^{2+} (25.8 meq/100 g) and a low Ca^{2+}/Mg^{2+} ratio (fig. 3B) stands out as a distinctive feature.

The remaining species, grouped in G4, are a heterogeneous group of Balearic island endemics (11) and more widespread taxa area (5, Mediterranean or W Mediterranean) (table 1), having low correlations to the three extracted axes. Statistically significant differential values include sandy soil texture (65.2%), low salinity (2.1 mS/cm) and a high proportion of carbonates (58.2%). (table 3).

Values of sand and carbonates for species of this group, unlike groups G2 and G3, have a lower variance between maximum values (84% sand, *L. tamarindanum* and 68.3% carbonate, *L. magallufianum*) and minimum values (51.4% sand, *L. validum* and 35.9%, carbonate, *L. balearicum*) (fig. 4B & C).

DISCUSSION

Marsh topography and morphology, and tidal regime, determinants of the distribution of general halophytes (Adam 1990, Sánchez et al. 1996, Sanderson et al. 2000, 2001, Bockelman et al. 2002, Silvestri et al. 2000), play here a secondary role as selective factors for plant colonization. Therefore, the different zoning patterns and distributions of *Limonium* species are linked to local elevation, short periods of flooding or soil salinity.

Soils show variations in their typology across the coastal areas studied. The precipitation and crusting of sulphates and carbonates is a very common feature in soils of arid and semiarid regions when lithological materials contain a high quantity of these components (Ruellan 1999, Boira et al. 2002). Although typologies of soils show variations across the littoral areas studied, it is rare to witness the presence of this type of crust in the saline environments of the Balearic Islands.

Apomictic reproduction is a common strategy among species that colonize habitats with variable environmental factors and in which soils are strongly saline. Often, both conditions coincide in the habitats studied, and species with this type of reproduction predominate. However, a relationship between polyploidy levels and soil salinity cannot be established.

Compared to other species of *Limonium* studied, the four species of group G1 (*L. heterospicatum*, *L. formenterae*, *L. retusum*, *L. wiedmannii*) are pioneers in the colonization of soils with high gypsum content. In the centre and SE of the Iberian Peninsula, natural gypsicolous substrates (evaporites) are colonized by species that have pioneer characteristics, such as: *Lepidium subulatum* L. (Brassicaceae), *Gypsophila struthium* Loefl. and *Herniaria fruticosa* L. (Caryophyllaceae), *Helianthemum squamatum* (L.) Pers. (Cistaceae), *Ononis tridentata* L. (Fabaceae) and *Thymus lacaitae* Pau (Lamiaceae). In these communities, some *Limonium* species – like *L. echioides*, *L. virgatum* or some endemics – are sporadically present (Boira et al. 2002). In contrast, in the Balearic Islands, populations of endemic *Limonium* species dominate in these anthropogenic, gypsophilous saline soils.

Total carbonates also reach high concentration levels with mean values of 59%. The differences of salt osmolarities and soil water contents for the four groups extracted exhibit spatial variation. Characteristic species of the G4 group – like *L. virgatum*, *L. gibertii*, *L. echioides*, *L. minutum*, *L. companyonis*, *L. ejulabilis* or *L. validum* – are typical of coastal cliff or salt marsh vegetation, being or not directly influenced by sea water. The same observations can be made for *L. camposanum*, *L. antonii-llorensii* and *L. migjornense* (G3), characteristic of coastal salt marshes but without experiencing a direct influence of marine water. For these two groups of species (G3, G4), a greater concentration of carbonates compared to chlorides and sulphates is due to the nature of skeletal soils, developed on dolomite and limestone rocks or alluvial saline sands.

According to Rabinowitz' scheme (1981), in which species were classified into categories according to their geographic range, habitat specificity and local population size, many *Limonium* species can be classified as rare, since they are "locally abundant, or scarce, in a specific habitat and restricted geographically". This is the case for numerous species that grow in salt marshes and reach optimum development in specific substrates. This is the case for group 1 and 3 species, particularly *L. formenterae*, *L. retusum*, *L. heterospicatum* and *L. wiedmannii*, which have a gypsicolous character. In natural conditions, their survival, development and conservation depend on salt extraction activities and the management of the waste products it generates. Also, in other salt marshes, the availability of halo-gypsophilous soils could be a determining factor for the conservation of *Limonium* populations.

SUPPLEMENTARY DATA

Supplementary data are available at *Plant Ecology and Evolution*, Supplementary Data Site (https://www.ingentaconnect.com/content/botbel/plecevo/supp-data) and consist of an Excel spreadsheet for the groups of *Limonium* species derived from floristic distances.

ACKNOWLEDGEMENTS

We would like to thank L. Cortés for his detailed comments and suggestions for the manuscript and C. Ornée for linguistic assistance. The Conselleria de Agricultura, Medi Ambient and Territori provided permissions to work at some study sites. We also appreciate the detailed comments by three anonymous reviewers on an earlier version of the manuscript.

REFERENCES

Acosta A., Ercole S., Stanisci A., De Patta Pillar V., Blasi C. (2007) Coastal vegetation zonation and dune morphology in some Mediterranean ecosystems. Journal of Coastal Research 23: 1518–1524. https://doi.org/10.2112/05-0589.1

Adam P. (1990) Saltmarsh ecology. Cambridge, Cambridge University Press. https://doi.org/10.1017/CBO9780511565328

Álvarez-Rogel J., Alcaraz F.A., Ortiz S.R. (2000) Soil salinity and moisture gradients and plant zonation in Mediterranean salt marshes of southeast Spain. Wetlands 20: 357–372. https://doi.org/10.1672/0277-5212(2000)020[0357:SSAMGA]2.0.CO;2

Álvarez-Rogel J., Ortiz S.R., Alcaraz F.A. (2001) Edaphic characterization and salt ionic composition influencing plant zonation in a semiarid Mediterranean salt marsh. Geoderma 99: 81–98. https://doi.org/10.1016/S0016-7061(00)00067-7

Artelari R., Georgiou O. (1999) Two new species of Limonium (Plumbaginaceae) from the island of Kithira (Greece). Botanical Journal of the Linnean Society 131: 399–415. https://doi.org/10.1111/j.1095-8339.1999.tb01522.x

Artelari R., Georgiou O. (2002) Biosystematic study of the genus Limonium (Plumbaginaceae) in the Aegean area, Greece. III. Limonium on the islands Kithira and Antikithira and the surrounding islets. Nordic Journal of Botany 22: 483–502. https://doi.org/10.1111/j.1756-1051.2002.tb01402.x

Baumberger T., Affre L., Croze T., Mesléard F. (2012a) Habitat requirements and population of the rare endangered Limonium girardianum in Mediterranean salt marshes. Flora 207: 283–293. https://doi.org/10.1016/j.flora.2011.11.008

Baumberger T., Croze T., Affre L., Mesléard F. (2012b) Co-occurring species indicate habitats of the rare Limonium girardianum. Plant Ecology and Evolution 145: 31–37. https://doi.org/10.5091/plecevo.2012.685

Beeftink W.G. (1977) The coastal salt marshes of western and northern Europe: an ecological and phytosociological approach. In: Chapman V.J. (ed.) Ecosystems of the World 1. Wet Coastal Ecosystems: 109–155. Amsterdam, Elsevier.

Bockelmann A.C., Bakker J.P., Neuhaus R., Lage J. (2002) The relation between vegetation zonation, elevation and inundation frequency in a Wadden Sea salt marsh. Aquatic Botany 73: 211–221. https://doi.org/10.1016/S0304-3770(02)00022-0

Boira H., Costa M., Batlle J., Soriano P., Loidi J., Samo J.A. (2002) Numerical revision of syntaxonomy and ecological characteristics of vegetation on gypsum substrates in Spain (C and SE). Ecologia Mediterranea 28: 39–53.

Bolòs O. (1967) Comunidades vegetales de las comarcas próximas al litoral situadas entre los ríos Llobregat y Segura. Memorias Real Academia Ciencias y Artes de Barcelona 42: 269–313.

Boorman L.A. (1971) Studies in salt marsh ecology with special reference to the genus Limonium. Journal of Ecology 59: 103–120. https://doi.org/10.2307/2258455

Braun-Blanquet J. (1964) Plant sociology. New York & London, Hafner Publishing Company.

Brullo S., Erben M. (2016) The genus Limonium (Plumbaginaceae) in Greece. Phytotaxa 240: 1–212. https://doi.org/10.11646/phytotaxa.240.1.1

Castro M., Rosselló J.A. (2007) Karyology of Limonium (Plumbaginaceae) species from the Balearic Islands and the western Iberian Peninsula. Botanical Journal of the Linnaean Society 155: 257–272. https://doi.org/10.1111/j.1095-8339.2007.00703.x

Castroviejo S., Cirujano S. (1980) Sarcocornietea en La Mancha (España). Anales del Jardín Botánico de Madrid 37: 143–154

Chapman V.J. (1974) Salt marshes and salt deserts of the world. Lehre, Verlag Von J. Cramer.

Chapman V.J. (1976) Coastal vegetation. Oxford, Pergamon Press. https://doi.org/10.1016/C2013-0-10099-2

Chapman H.D., Pratt P.F. (1961) Methods of analysis for soil plants and water. Berkeley, University of California.

Clements F.E. (1916) Plant succession: an analysis of the development of vegetation. Washington DC., Camegie Institution. https://doi.org/10.5962/bhl.title.56234

Costa M., Boira H. (1981) La vegetación costera valenciana: los saladares. Anales del Jardín Botánico de Madrid 38: 233–24.

Costa C.S.B., Marangoni J.C., Azevedo A.M.G. (2003) Plant zonation in irregularly flooded salt marshes: relative importance of stress tolerance and biologica1 interactions. Journal of Ecology 91: 951–965. https://doi.org/10.1046/j.1365-2745.2003.00821.x

Cowan R., Ingrouille M.J., Lledó M.D. (1998) The taxonomic treatment of agamosperms in the genus Limonium Mill. (Plumbaginaceae). Folia Geobotanica 33: 353–366. https://doi.org/10.1007/BF03216212

Erben M. (1979) Karyotype differentiation and its consequences in Mediterranean Limonium. Webbia 34: 409–417. https://doi.org/10.1080/00837792.1979.10670178

Erben M. (1989) Bemerkungen zur Taxonomie der Gattung Limonium V. Mitteilungen der Botanischen Staatssammlung München 28: 313–417.

Erben M. (1993) Limonium. In: Castroviejo S., Aedo C., Cirujano S. et al. (eds) Flora Iberica 3: 2–143. Madrid, Real Jardín Botánico-C.S.I.C.

Fernández-García N., Martínez V., Carvajal M. (2004) Effect of salinity on growth, mineral composition, and water relations of grafted tomato plants. Journal of Plant Nutrition and Soil Science 167: 616–622. https://doi.org/10.1002/jpln.200420416

Flowers T.J., Colmer T.D. (2008) Salinity tolerance in halophytes. New Phytologist 179: 945–963. https://doi.org/10.1111/j.1469-8137.2008.02531.x

Fornós J.J. (2011) Eolianitas y dunas cuaternarias en las Islas Baleares. In: Sanjaume E., Gracia F.J. (eds) Las dunas en España: 307–330. Sociedad Española de Geomorfología.

Girija C., Smith B., Swamy P. (2002) Interactive effects of sodium chloride and calcium chloride on the accumulation of proline and glycinebetaine in peanut (Arachis hypogaea L.). Environmental and Experimental Botany 47: 1–10. https://doi.org/10.1016/S0098-8472(01)00096-X

Greuter W., Burdet H.M., Long G. (1989) Med-Checklist, Vol. 4. Geneva, Editions des Conservatoire et Jardin botaniques de la Ville de Genève.

Llorens L. (1985a) El género Limonium en la isla de Formentera. Lazaroa 8: 69–83.

Llorens L. (1985b) Revisión sistemático-taximétrica del género Limonium Miller en la isla de Mallorca, I. Lazaroa 8: 11–68.

Llorens L. (1986) La vegetación de los saladares de la isla de Formentera (Baleares). Anales del Jardín Botánico de Madrid 42: 469–479.

Llorens L., Tébar J. (1988) Limonium escarrei and Limonium boirae Llorens & Tébar, two new species for the island of Majorca (Balearic Islands). Anales del Jardín Botánico de Madrid 45: 173–180.

McCune B., Mefford M.J. (2011) PC-ORD. Multivariate analysis of ecological data.Version 6.0. Oregon, MJM Software.

Nelson D.W., Sommers L.E. (1996) Total carbon, organic carbon, and organic matter. In: Sparks D.L. et al. (eds) Methods of soil analysis. Part 3. Chemical methods, SSSA Book Series No. 5: 961–1010. Madison, WI, SSSA & ASA. https://doi.org/10.2136/sssabookser5.3.c34

Naqvi S.S.M., Mumtaz S., Shereen A., Khan M.A., Khan A.H. (1997) Role of abscisic acid in regulation of wheat, seedling growth under salinity stress. Biologia Plantarum 39: 453–456. https://doi.org/10.1023/A:1001005031886

Odum E.P. (1983) Basic ecology. Philadelphia, PA, CBS College Publishing.

Palacios C., Rosselló J.A., González-Candelas F. (2000) Study of the evolutionary relationships among Limonium species (Plumbaginaceae) using nuclear and cytoplasmic molecular markers. Molecular Phylogenetics and Evolution 14: 232–249. https://doi.org/10.1006/mpev.1999.0690

Pavon D. (2005) Note sur le genre Limonium Miller dans le département des Bouches–du–Rhône. Bulletin de la Société Linnéenne de Provence 56: 135–139.

Pignatti S. (1982) Flora d'Italia vol. 2: 302–319. Bologna, Edagricole.

Rabinowitz D. (1981) Seven forms of rarity. In: Synge H. (ed.) The biological aspects of rare plant conservation: 205–218. New York, John Wiley & Sons Ltd.

Rzasa S, Owczarzak W. (2013) Methods for the granulometric analysis of soil for science and practice. Polish Journal of Soil Science 46(1): 1–50.

Redfield A.C. (1972) Development of a New England salt marsh. Ecological Monographs 42: 201–237. https://doi.org/10.2307/1942263

Richards L.A. (1954) Diagnosis and improvement of saline and alkali soils. U.S. Department of Agriculture Handbook 60. Washington, US Government Printing Office.

Rivas-Martínez S. (1984) Pisos bioclimáticos de España. Lazaroa 5: 33–43.

Ruellan A. (1999) The main rules of soil distribution in the Mediterranean world. 6th International Meeting of Soils with Mediterranean Type of Climate. Barcelona, Spain. Extended Abstracts: 41–42. UB Publicacions.

Sáez L. (2005) Limonium Mill. (Plumbaginaceae) In: Bolòs O., Vigo J., Masalles R.M., Ninot J.M. (eds) Flora manual dels països catalans: 622–636. Pòrtic.

St. Omer L. (2004) Small-scale resource heterogeneity among halophytic plant species in an upper salt marsh community. Aquatic Botany 78: 337–348. https://doi.org/10.1016/j.aquabot.2003.12.002

Sánchez J.M., Izco J., Medrano M. (1996) Relationships between vegetation zonation and altitude in a salt-marsh system in northwest Spain. Journal of Vegetation Science 7: 695–702. https://doi.org/10.2307/3236381

Sanderson E.W., Ustin S.L., Foin T.C. (2000) The influence of tidal channels on the distribution of salt marsh plant species in Pataluma Marsh, CA, USA. Plant Ecology 146: 29–41. https://doi.org/10.1023/A:1009882110988

Sanderson E.W., Foin T.C., Ustin S.L. (2001) A simple empirical model of salt marsh plant spatial distribution with respect to a tidal channel network. Ecological Modelling 139: 293–307. https://doi.org/10.1016/S0304-3800(01)00253-8

Silvestri S., Marani M., Rinaldo A., Marani A. (2000) Vegetazione alofila e morfologia lagunare. Atti dell'Istituto Veneto di Scienze, Lettere ed Arti 68: 333–359.

Soil Survey Staff (2014) Kellog Soil Survey Laboratory methods manual. Soil Survey Investigations Report No. 42, Version 5.0. Lincoln, NE, U.S. Department of Agriculture, Natural Resources Conservation Service.

ter Braak C.J.F. (1987) The analysis of vegetation-environment relationships by canonical correspondence analysis. Vegetatio 69: 69–77. https://doi.org/10.1007/BF00038688

van Wijnen H.J., Bakker J.P, de Vries Y. (1997) Twenty years of salt marsh succession on a Dutch coastal barrier island. Journal of Coastal Conservation 3: 9–18. https://doi.org/10.1007/BF02908174

Vilà J. (1953) Ibiza y Formentera, islas de la sal. Estudios Geográficos CSIC 14: 363–408.

Vilà J. (2000) Las salinas de Ibiza y Formentera. Territoris 3: 191–204.

Walkley A., Black I.A. (1934) An examination of the Degtjareff method for determining soil organic matter, a proposed modification of the chromic acid titration method. Soil Science 37: 29–38. https://doi.org/10.1097/00010694-193401000-00003

Manuscript received 24 Jul. 2017; accepted in revised version 19 Jun. 2018.

Communicating Editor: Nicolas Barbier.