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Sarcocornia fruticosa, a Potential Candidate for Saline Agriculture: Antioxidant Levels in Relation to Environmental Conditions in the Eastern Iberian Peninsula

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Abstract: Sustainable crop production requires an innovative approach due to increasing soil salinisation and decreasing freshwater availability. One promising strategy is the domestication of naturally salt-tolerant plant species with commercial potential. *Sarcocornia fruticosa* is a highly salt-tolerant halophyte, common in Mediterranean marshes, which may hold promise for biosaline agriculture. This study included 11 populations of this species spread over the territory of the Valencian Community in eastern Spain. Climatic data for each locality were obtained from the nearest meteorological stations. Soil analyses included texture, pH, electroconductivity, organic carbon and organic matter. Biochemical analyses on wild-sampled plant material focused on antioxidant compounds, such as carotenoids, phenolics, flavonoids and proline with malondialdehyde (MDA) used as a marker of oxidative stress. All variables (climatic, edaphic and biochemical) were evaluated together using Principal Component Analysis and Spearman correlation. The results obtained indicated some climatic differences in terms of mean annual precipitation, with a clear N-S gradient and considerable edaphic variability. However, none of the environmental conditions showed a clear correlation with plant biochemical characteristics. Significant differences in the levels of phenolic compounds, flavonoids and MDA between populations were probably due to genetic factors and cannot be explained as a response to environmental conditions.

Keywords: halophytes; climatic conditions; soil type; antioxidants; correlations

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1. Introduction

The genus *Sarcocornia* A.J. Scott belongs to the family Amaranthaceae (formerly Chenopodiaceae), subfamily Salicornioideae Kostel. This subfamily comprises 16 genera [1], all characterised by morphological and physiological adaptations, which facilitate their development in extreme habitats, especially saline environments. These adaptations result in morphological homogenisation, with a reduction in leaf size and an increase in the succulence of stems, which leads to taxonomic difficulties [2]. Scott described this genus [3] as grouping shrubs, erect or prostrate, much branched, sometimes rooted at the nodes, with flowers inserted at the same level, seeds without perisperm and with membranous pericarp and the seed testa covered with hairs. This description differentiated *Sarcocornia* from the annual species of the genus *Salicornia* L. and the related genus *Arthrocnemum* Moq., which has glabrous and shiny seeds with perisperm. However, in more recent taxonomic

revisions, all *Sarcocornia* species were merged under *Salicornia* L. [4]. Also under question is the taxonomic status of *Sarcocornia fruticosa* (L.) A.J. Scott, a common species in salt marshes throughout the Western Mediterranean region. A relatively recent study [5] suggests that this species is not present in the Iberian Peninsula and that the individuals found in Iberian saline habitats belong to a newly described (but not yet generally widely acknowledged) species, *S. lagascae* Fuente, Rufo & Sánchez Mata. However, as the object of this study is not taxonomic, we will follow the most used, traditional nomenclature and name the species *S. fruticosa*.

Sarcocornia fruticosa is found in coastal and inland marshes up to 600 m above sea level. It is a halophyte tolerating high salinity levels and its adaptation to saline environments is based mainly on the accumulation of salts in its tissues. This morphological adaptation results in succulence in their stems and leaves, allowing them to accumulate and sequester salts to avoid toxicity and to compensate for differences in osmotic pressure with the soil, a typical strategy of succulent halophytes [6]. The species is considered to be among the most salt-tolerant halophytes [7] and appears to have adapted to a wide range of salinities, including extremely hypersaline conditions, indicating considerable physiological plasticity [8]. *Sarcocornia fruticosa* is common in salt marsh plant communities, which can sometimes be inundated by brackish water of marine origin but can also occur in inland endorheic zones (areas with closed drainage) and are therefore subject to periodic flooding, tidal abrasion and deposition, and salt stress [9]. The species frequently forms monospecific stands in areas where flooding periods are prolonged or where salt concentrations are too high for other plants to survive.

The habitats in which the genus *Sarcocornia* occurs are highly fragile. It grows on saline soils, usually near the coast and in salt marshes in arid and semi-arid regions throughout the world [10], habitats that are highly fragmented and seriously threatened by anthropogenic activities [11]. These ecosystems, due to their reduced surface area worldwide, are of great value because of their scarcity and uniqueness. Furthermore, from a botanical point of view, the flora and vegetation of these environments are very special and of great interest due to their capacity to develop in soil with such particular and restrictive characteristics [12].

The number of studies on the recruitment of wild halophytes with economic potential has increased considerably in recent decades. A range of cultivation systems has been developed for the use of halophytes in agriculture, biofuel production, purification of saline effluents in constructed wetlands, gardening and gourmet vegetable cultivation, among other applications [13].

For this reason, the tolerance to extreme salinity makes some members of the genera *Sarcocornia* and *Salicornia* be considered promising crops or fodder plants in regions with salt accumulation problems [14–17]. The species under study could, therefore, be a solution for agriculture in areas where other species with food potential do not grow due to salinity. Another possible use of this species is in the restoration of saline soils or even in the rehabilitation of polluted environments [18–20].

In this study, we analysed the levels of some antioxidant compounds in plants collected in their natural habitats in the Valencian Community, eastern Spain. Halophytes are known to have the ability to synthesise and accumulate metabolites to mitigate the effect of salt stress, and many of these compounds, such as antioxidants, have a beneficial effect on human health. Halophytes represent an important but still under-exploited resource of nutraceuticals [21,22].

The objectives of this study were to analyse the concentration of photosynthetic pigments, total phenolic compounds, total flavonoids, malondialdehyde and proline in plant material sampled in the wild from 11 marshes in eastern Spain and to correlate biochemical results with climatic conditions and soil characteristics at the sampling sites. This approach aimed to explore how different environmental variables influence the biochemical profiles of the plants.

2. Materials and Methods

2.1. Area of Study

The study area covers the three provinces of the Valencian Community in Eastern Spain. Soil and plant material were sampled from 11 salt marshes, all situated in coastal areas (Table 1).

Table 1. Analysed populations of *Sarcocornia fruticosa* from SE Spain and their locations.

Province	Locality	Code	Latitude	Longitude
Castellón	Torreblanca	TB	40 10 32.4834 N	0 11 33.4948 E
Castellón	Almenara	AL	39 43 03.3302 N	0 11 50.1489 W
Valencia	Marjal del Moro	MM	39 37 08.0000 N	0 15 24.0000 W
Valencia	Mallada Redona	MR	39 22 11.2800 N	0 19 26.7112 W
Valencia	Mallada Llarga	ML	39 21 06.8742 N	0 19 04.2744 W
Alicante	Aigua Amarga	AA	38 17 10.3408 N	0 31 21.5077 W
Alicante	Clot de Galvany 1	C1	38 14 58.4565 N	0 31 55.5632 W
Alicante	Clot de Galvany 2	C2	38 14 40.1462 N	0 32 23.8684 W
Alicante	Fondo	FO	38 12 27.3806 N	0 45 59.9646 W
Alicante	Salinas de Santa Pola	SP	38 11 02.0012 N	0 36 55.0732 W
Alicante	Torrevieja	TV	38 01 06.8000 N	0 40 18.6000 W

2.2. Climatic Analysis

Climatic data for the period 2000–2023 were obtained from the nearest meteorological stations (indicated in Table 2), provided by the Agroclimatic Information System for Irrigation (SIAR) [23], of the Spanish Ministry of Environment, Rural and Marine Affairs (MARM). Mean temperatures, mean solar radiation, annual precipitation and potential evapotranspiration were calculated from monthly data from the period between 2000 and 2023.

Table 2. Values of the climatic variables at the sampling sites of soil and plant material. Abbreviations: T, annual mean temperature; Rad, mean solar radiation; P, annual precipitation; PET, annual potential evapotranspiration. Values were calculated for the period 2000–2023 from data provided by SIAR 2024.

Meteorological Station	Area Code	T (°C)	Rad (MJ/m^2)	P (mm)	PET (mm)
Benavites	AL	17.36	16.80	466	1079
Ribera de Cabanes	TB	17.28	16.02	481	1078
Sagunto	MM	17.94	16.53	431	1177
Benifayo	ML, MR	18.27	17.34	472	1348
Elche	C1, C2, AA, SP	18.78	17.64	278	1191
Catral	FO	17.91	16.65	298	1151
Pilar de la Horadada	TV	19.07	18.23	355	1210

2.3. Soil Analysis

Soil samples were taken at a depth of 0–15 cm from the different study areas where plants were sampled. Three soil samples were collected from each location. After collection, the samples were weighed and left to air dry on a tray, spread out on clean, dry filter paper in a thin layer. To homogenise the dried samples, they were ground with a roller and then passed through a 2 mm sieve.

The soil texture, which expresses the proportions, by weight, of the various sizes of inorganic particles smaller than 2 mm, was analysed by the hydrometer method [24]. The soil pH and electroconductivity were measured in a saturated extract by a Crison pH-meter Basic 20 and a Crison Conductimeter Basic 30 (Crison Instruments S.A., Barcelona, Spain), respectively. The Walkey–Black, or wet combustion method, was used to determine the oxidisable organic matter content of the soil expressed as a percentage (OM) using the

following formulas: (1) and (2). This method calculates the percentage of organic carbon (OC) in the soil. The organic matter content (OM) is then estimated indirectly by analysing the OC using a Bernard Calcimeter.

$$\%\ \text{Organic Carbon (OC)} = \frac{\left[\left(10 - \left(\text{mL } \textit{Ferrous Sulfate} \times \frac{10}{\text{mL } \textit{Blank Ferrous Sulfate}}\right) \times 1.3 \times 1000\right]}{\text{Soil Weight(gr)}} \quad (1)$$

$$\%\ \text{Organic Matter(OM)} = \%\ \text{Organic Carbon(OC)} \times 1.724 \quad (2)$$

2.4. Biochemical Analysis

Plant material was sampled from five individuals at each location. A fraction of the plant material was stored at −80 °C for biochemical analysis, and the remaining material was dried in an oven at 65 °C until constant weight was reached. Water contents (WCs) were expressed as percentages of fresh weight.

Chlorophylls *a* and *b* (Chl a, Chl b) and total carotenoids (Caro) were determined by the classical protocol developed by Lichtenthaler & Wellburn [25]. A total of 10 mL of ice-cold 80% (*v*/*v*) acetone was used to extract pigments from 0.05 g of fresh leaf material. After mixing overnight and centrifuging for 10 min at 12,000 rpm, the supernatant was collected, and its absorbance was measured at 663, 646 and 470 nm. Chl a, Chl b and Caro concentrations were calculated using the described equations [25], and their contents were expressed in mg g^{-1} DW. Total phenolic compounds (TPCs) and total flavonoid (TF) concentrations were determined in 80% (*v*/*v*) methanol extracts from 0.05 g of fresh leaf material. TPC was measured according to Blainski et al. [26] by its reaction with the Folin–Ciocalteu reagent and sodium carbonate. Absorbance measurements were made at 765 nm and TPC concentrations were expressed as equivalents of gallic acid (mg eq. GA g^{-1} DW). For quantification of TF, the extracts were combined with sodium nitrite and aluminium chloride in an alkaline environment, and absorbance was measured at 510 nm in accordance with Zhishen et al. [27]. The concentrations of TF were expressed as equivalents of catechin (mg eq. C. g^{-1} DW).

The malondialdehyde (MDA) contents were determined following the method described by Hodges et al. [28]. Leaf methanol extracts (80% *v*/*v*) were supplemented with 0.5% thiobarbituric acid (TBA) in 20% trichloroacetic acid (TCA), or with 20% TCA without TBA for the controls and incubated for 15 min at 95 °C in a water bath. The reaction was stopped on ice, and the absorbance was measured at 440, 600 and 532 nm. The MDA concentrations were calculated using the equations described [29].

Proline (Pro) was extracted from 0.05 g of fresh leaf material with 2 mL of 3% (*w*/*v*) sulphosalicylic acid and quantified according to the ninhydrin method by Bates et al. [30]. The extract mixed with acid ninhydrin was heated at 95 °C in a water bath for one hour, cooled on ice and extracted with toluene; the absorbance of the organic phase was measured at 520 nm. Samples with known Pro amounts were assayed in parallel to obtain a standard curve. Pro concentrations were expressed as μmol g^{-1} DW.

2.5. Statistical Analysis

Data were analysed by the programs SPSS v. 16 and SYSTAT v. XVI. Before the analysis of variance, the Shapiro–Wilk test was used to check for the validity of normality assumption, and Levene's test was used for testing the homogeneity of variance. If the ANOVA requirements were accomplished, the significance of the differences among treatments was tested by a one-way ANOVA at the 95% confidence level and post hoc comparisons were made using the Student–Newman–Keuls' test. Spearman's rank correlation was performed using RStudio version 4.3.1 to evaluate the relationships between variables. The *psych* and *corrplot* packages were used to calculate and visualise the correlation matrix, while the *ggcorrplot* package was used to create detailed correlation plots with labelled coefficients and a colour gradient for enhanced clarity.

3. Results

3.1. Climatic Analysis

All areas exhibited similar climatic conditions, typical for the Mediterranean climate, with mean temperatures ranging from 17 to 19 °C and comparable average minimum and maximum temperatures (Table 2).

The highest temperatures occurred in summer, coinciding with a drastic reduction in precipitation, characteristic of the Mediterranean climate. Nevertheless, the amount of precipitation differs, ranging from values below 300 mm in the southern localities (C1, C2; AA, SP and FO) to maximum values of 481 in the province of Castellón, in the N of the area where the TB population is located.

Figure 1 shows climate charts for three locations across the three different provinces of the Valencian Community, calculated for the period 2000–2023 using data provided by SIAR 2024. As expected, the pattern is very similar, but there is a reduction in precipitation according to the N-S gradient (top–bottom on the graph).

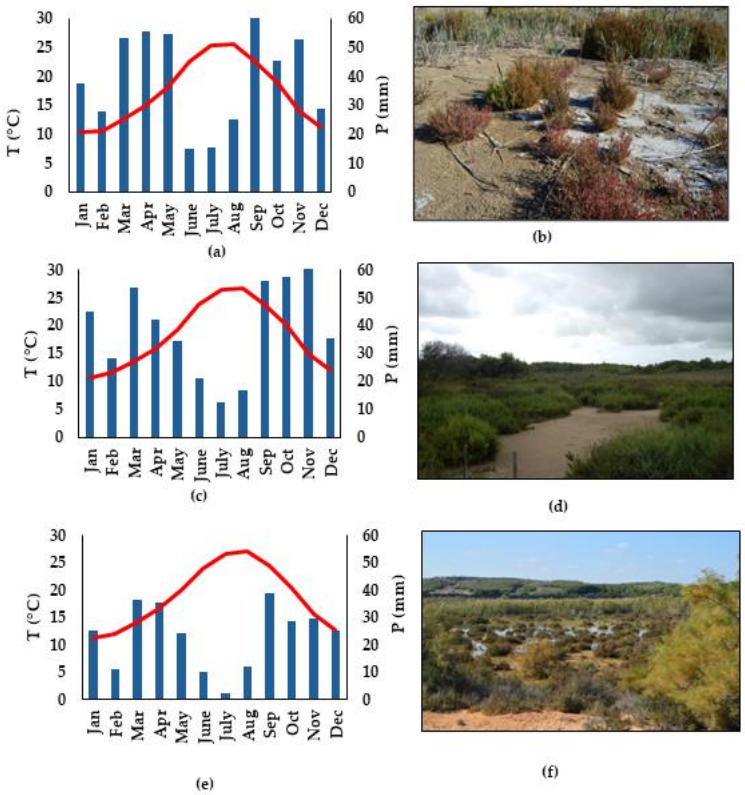

Figure 1. Climatic charts and habitat images of three sampling areas: TB, Torreblanca (**a**,**b**), ML, Mallada Llarga (**c**,**d**) and C1, Clot de Galvany1. Blue histograms represent precipitation (mm), and red line the mean temperature (°C). Values were calculated for the period 2000–2023 using data provided by SIAR 2024 from the following meteorological stations: (**a**,**b**) Ribera de Cabanes, Castellón province, (**c**,**d**) Benifayo, Valencia province, and (**e**,**f**) Elche, Alicante province.

3.2. Soil Analysis

Soil analysis included both physical (percentages of sand, silt and clay) and chemical characteristics (pH, electric conductivity, organic carbon and organic matter). Table 3 shows the proportions by weight of the different particle sizes, which allowed for the calculation of the soil texture. The majority of areas were classified as sandy loam (AL, MM, TV and C2), three had a sand texture (TB, ML, MR), the other three were silt loam (C1, FO, AA) and, finally, only one silt (SP).

Table 3. Soil characteristics of the 11 sampling areas. Values represent means ± SE (n = 3). Different lowercase letters indicate significant differences according to the Tukey's test at a 95% confidence level.

Code	Sand (%)	Silt (%)	Clay (%)	pH	EC (dSm^{-1})	OC (%)	OM (%)
AL	67.00 ± 1.15 ^{b}	33 ± 1.73 ^{cd}	0.00 ± 0.00 ^{d}	7.54 ± 0.29 ^{b}	67.26 ± 1.15 ^{c}	10.78 ± 0.58 ^{a}	18.59 ± 1.15 ^{a}
TB	92.50 ± 0.86 ^{a}	7.50 ± 0.86 ^{e}	0.00 ± 0.00 ^{d}	8.41 ± 0.25 ^{a}	17.33 ± 2.32 ^{de}	7.92 ± 0.02 ^{e}	13.65 ± 0.03 ^{e}
MM	67.00 ± 0.58 ^{b}	23.00 ± 0.58 ^{d}	10.00 ± 0.00 ^{a}	7.36 ± 0.11 ^{b}	76.32 ± 0.05 ^{bc}	8.98 ± 0.11 ^{c}	15.47 ± 0.23 ^{cd}
ML	95.00 ± 1.29 ^{a}	4.66 ± 1.09 ^{d}	0.33 ± 0.22 ^{cd}	8.60 ± 0.13 ^{a}	25.46 ± 7.03 ^{de}	8.01 ± 0.07 ^{e}	13.82 ± 0.12 ^{e}
MR	94.66 ± 0.33 ^{a}	5.33 ± 0.33 ^{e}	0.00 ± 0.00 ^{d}	8.29 ± 0.04 ^{a}	10.93 ± 1.64 ^{e}	8.33 ± 0.05 ^{cd}	14.37 ± 0.08 ^{de}
C1	58.33 ± 8.21 ^{b}	41.67 ± 8.21 ^{c}	0.00 ± 0.00 ^{d}	7.37 ± 0.24 ^{b}	80.29 ± 4.89 ^{bc}	9.91 ± 0.28 ^{ab}	17.09 ± 0.48 ^{ab}
C2	30.67 ± 3.81 ^{d}	67.00 ± 4.50 ^{b}	2.33 ± 0.72 ^{cd}	7.64 ± 0.06 ^{b}	12.89 ± 1.57 ^{e}	8.78 ± 0.34 ^{c}	15.15 ± 0.60 ^{d}
AA	28.66 ± 17.1 ^{c}	69.33 ± 15.5 ^{b}	2.00 ± 2.00 ^{cd}	7.47 ± 0.06 ^{b}	43.09 ± 7.57 ^{cd}	9.21 ± 0.38 ^{bc}	15.88 ± 0.66 ^{c}
SP	10.00 ± 0.003 ^{d}	85.00 ± 0.58 ^{a}	5.00 ± 0.58 ^{b}	7.26 ± 0.00 ^{b}	100.65 ± 12.2 ^{ab}	8.27 ± 0.06 ^{de}	14.26 ± 0.11 ^{de}
FO	25.00 ± 0.58 ^{d}	75.00 ± 0.58 ^{ab}	0.00 ± 0.00 ^{d}	7.41 ± 0.12 ^{b}	116.18 ± 0.58 ^{a}	9.58 ± 0.23 ^{b}	16.52 ± 1.15 ^{bc}
TV	68.67 ± 1.33 ^{b}	23.00 ± 1.00 ^{de}	8.33 ± 1.12 ^{a}	8.15 ± 0.11 ^{a}	19.18 ± 5.44 ^{de}	10.54 ± 0.48 ^{a}	18.17 ± 0.82 ^{a}

The pH of the soil in the areas studied was, in all cases, basic, ranging from 7.26 to 8.60. These values can, therefore, be considered to range from moderately basic to alkaline.

The electric conductivity varied largely from 10.93 dS m^{-1} at MR to a maximum of 116.18 at FO. Two areas (MR and C2) could be classified as strongly saline (with EC from 8–16 dSm^{-1}), whereas all others as extremely saline (over 16 dSm^{-1}) according to the USSL classification [31].

Soil organic matter consists of micro-organisms, undecomposed remains of plants and animals, and materials resulting from the decomposition of these remains by the action of micro-organisms and the environment in general. A common characteristic of all organic matter is the presence of carbon (C) in its composition, which is called organic C. Three other plant macronutrients, N, P and S, are constituents of organic matter, as well as other micronutrients such as Fe, Cu, Zn and Mn. The values obtained for organic carbon varied from approximately 8% to 11% and that of organic matter from 13% to 18%. All samples presented a very high content of organic matter, as percentages above 3.6% are considered very high levels [32].

3.3. Biochemical Analysis

Several compounds with value in human nutrition were analysed to assess the potential use of *S. fruticosa* as a functional food: carotenoids (quantified together with chlorophyll *a* and *b*), total phenols and total flavonoids. In addition, the analysis included proline, an osmolyte with antioxidant function, and malondialdehyde, a marker of oxidative stress.

For expressing the concentrations on a dry weight basis and for supporting correlations with environmental conditions, the water content of the samples was measured (Figure 2a). Although all values were high (above 75%), typical for succulent plants, significant variations between populations were registered, from a minimum water content of 77.73% in AA (Alicante province) to 84.69% in TB (Castellón province).

Regarding MDA concentrations, significantly lower values were detected for the populations C1 and C2 (Figure 2b), both of which were located in the Clot de Galvany area despite high differences in salinity levels. Variations were also significant for phenolic and flavonoid levels. Phenolic concentrations ranged from 33–34 μg g^{-1}DW in MR, TV and C2 to over 60 μg g^{-1}DW in MM. Flavonoid concentrations ranged from the lowest values of 65 and 72 μg g^{-1}DW in AL and C2, respectively, to 137 μg g^{-1}DW in ML and 138 μg g^{-1}DW in AA.

Based on the photosynthetic pigments and proline concentrations shown in Table 4, we did not detect any significant variations between populations.

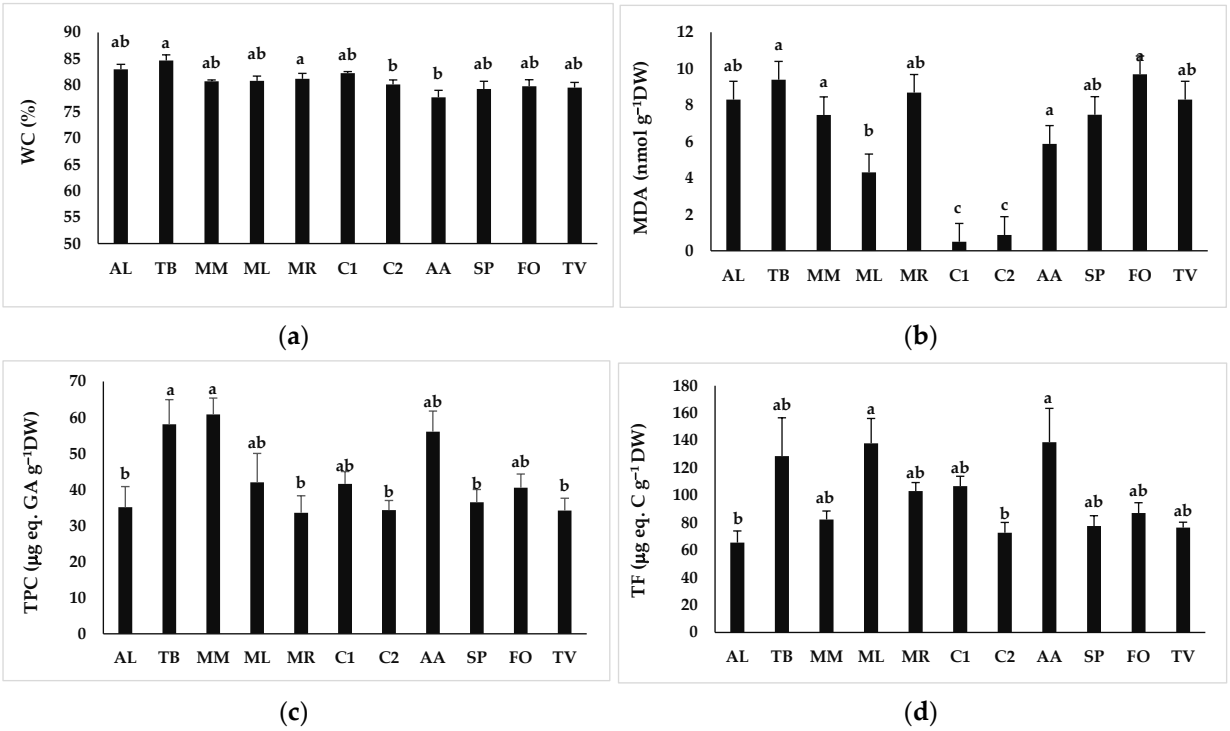

Figure 2. Water content (**a**), malondialdehyde (**b**), total phenolic compounds (**c**) and total flavonoid concentrations (**d**) in plants sampled in the wild in 11 locations in Valencian salt marshes. Bars represent mean values ± SE (n = 5). Different lowercase letters above the bars indicate significant differences according to the Student–Newman–Keuls' test at 95% confidence level.

Table 4. Chlorophyll *a*, chlorophyll *b*, carotenoids and proline concentrations in plants sampled in the wild in 11 locations in Valencian salt marshes. Mean values ± SE (n = 5).

	Chl *a* (mg g^{-1}DW)	Chl *b* (mg g^{-1}DW)	Caro (mg g^{-1}DW)	Pro (µmol g^{-1}DW)
AL	0.34 ± 0.07	0.21 ± 0.02	0.11 ± 0.02	1.13 ± 0.10
TB	0.24 ± 0.05	0.18 ± 0.01	0.09 ± 0.01	1.32 ± 0.31
MM	0.28 ± 0.07	0.20 ± 0.02	0.13 ± 0.02	1.08 ± 0.15
ML	0.20 ± 0.04	0.18 ± 0.01	0.09 ± 0.01	0.96 ± 0.09
MR	0.28 ± 0.07	0.21 ± 0.02	0.09 ± 0.01	0.95 ± 0.10
C1	0.46 ± 0.08	0.25 ± 0.02	0.10 ± 0.01	0.99 ± 0.05
C2	0.31 ± 0.07	0.24 ± 0.02	0.09 ± 0.03	1.09 ± 0.10
AA	0.38 ± 0.13	0.24 ± 0.04	0.07 ± 0.02	0.95 ± 0.09
SP	0.33 ± 0.08	0.23 ± 0.03	0.08 ± 0.02	1.53 ± 0.24
FO	0.41 ± 0.06	0.26 ± 0.02	0.07 ± 0.02	0.92 ± 0.07
TV	0.41 ± 0.11	0.23 ± 0.05	0.04 ± 0.02	1.13 ± 0.12

3.4. Principal Component and Correlation Analysis

A Principal Component Analysis was performed with all variables analysed, using mean values for soil and biochemical parameters (Figure 3). The PCA detected six components out of 19 with eigenvalues higher than 1, the first two covering 54.43% of the variability, with the first one explaining 39.52% and the second an additional 14.90%. The first component was mostly correlated positively with the concentrations of chlorophylls *a* and *b* in the plants and the percentage of silt in the soil and negatively with the annual rainfall. The second component was correlated with the electric conductivity, mean temperature and mean solar radiation (Table 5).

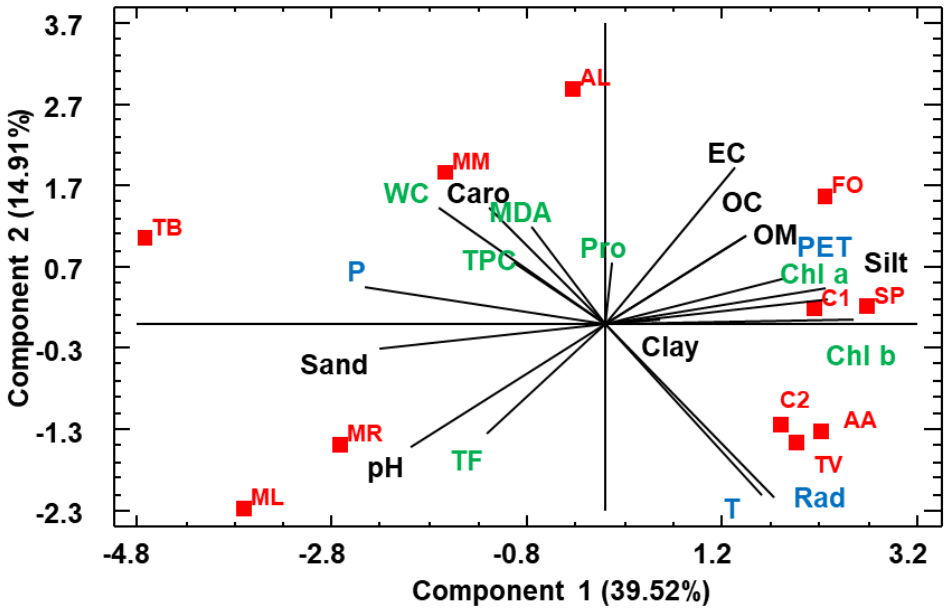

Figure 3. Principal Component Analysis conducted with climatic parameters (blue), soil characteristics (black) and biochemical traits (green) analysed in plant material sampled from 11 locations (red) in the region of Valencia in E Spain. Abbreviations as in Table 4.

Table 5. Component weights in the PCA performed with all analysed variables. Abbreviations: EC, soil electric conductivity; OC, organic carbon; OM, organic matter; T, temperature; Rad, solar radiation, P, precipitation, PET, potential evapotranspiration; TPC, total phenolic compounds; TF, total flavonoids; WC, water content; Chl *a*, chlorophyll *a*; Chl *b*, chlorophyll *b*; Caro, carotenoids; MDA, malondialdehyde; Pro, proline. Biochemical traits analysed were not conclusive in distinguishing among the analysed population.

Variable	Component 1	Component 2
Sand	−0.313	−0.059
Silt	0.308	0.059
Clay	0.076	0.012
pH	−0.268	−0.294
EC	0.179	0.371
OC	0.194	0.210
OM	0.195	0.210
T	0.235	−0.412
Rad	0.217	−0.408
P	−0.334	0.089
PET	0.249	0.107
WC	−0.229	0.276
TF	−0.162	−0.263
TPC	−0.127	0.147
Chl *a*	0.304	0.082
Chl *b*	0.345	0.010
Caro	−0.160	0.275
MDA	−0.101	0.229
Pro	0.009	0.143

The 11 populations analysed were dispersed onto the two axes of the scatterplot, mostly according to climatic and edaphic variables (Figure 3). There was a clear separation of populations along the first component axis, those from the southern Alicante province, with lower precipitation, on the right side of the graph, from the remaining ones from Valencia and Castellón on the central and left sides of the graph. Further, populations were dispersed along the second component axis according to soil characteristics, such as

electric conductivity, texture (percentages of sand, silt and clay) and organic carbon and organic matter.

A Spearman correlation was performed in addition to detect possible correlations between analysed variables (Figure 4). Strong correlations were detected between climatic parameters: mean temperature positively correlated with solar radiation (0.99) and the latter with potential evapotranspiration (0.87); precipitation negatively correlated with potential evapotranspiration (−0.76). Some significant correlations were found for soil characteristics as well; percentages of sand and silt were negatively correlated with each other (−1), and sand with electric conductivity (−0.83). The succulence of plants, measured as their percentage of water content, was slightly positively correlated with the rainfall (0.74). Some biochemical traits were also correlated, such as chlorophyll *a* and *b*, which showed a strong positive correlation (0.98), total phenolic compounds a positive one with pH (0.73) and negative with chlorophyll *a* (−0.82) and *b* (−0.85) and MDA negative correlations with solar radiation (−0.62) and mean temperature (−0.57).

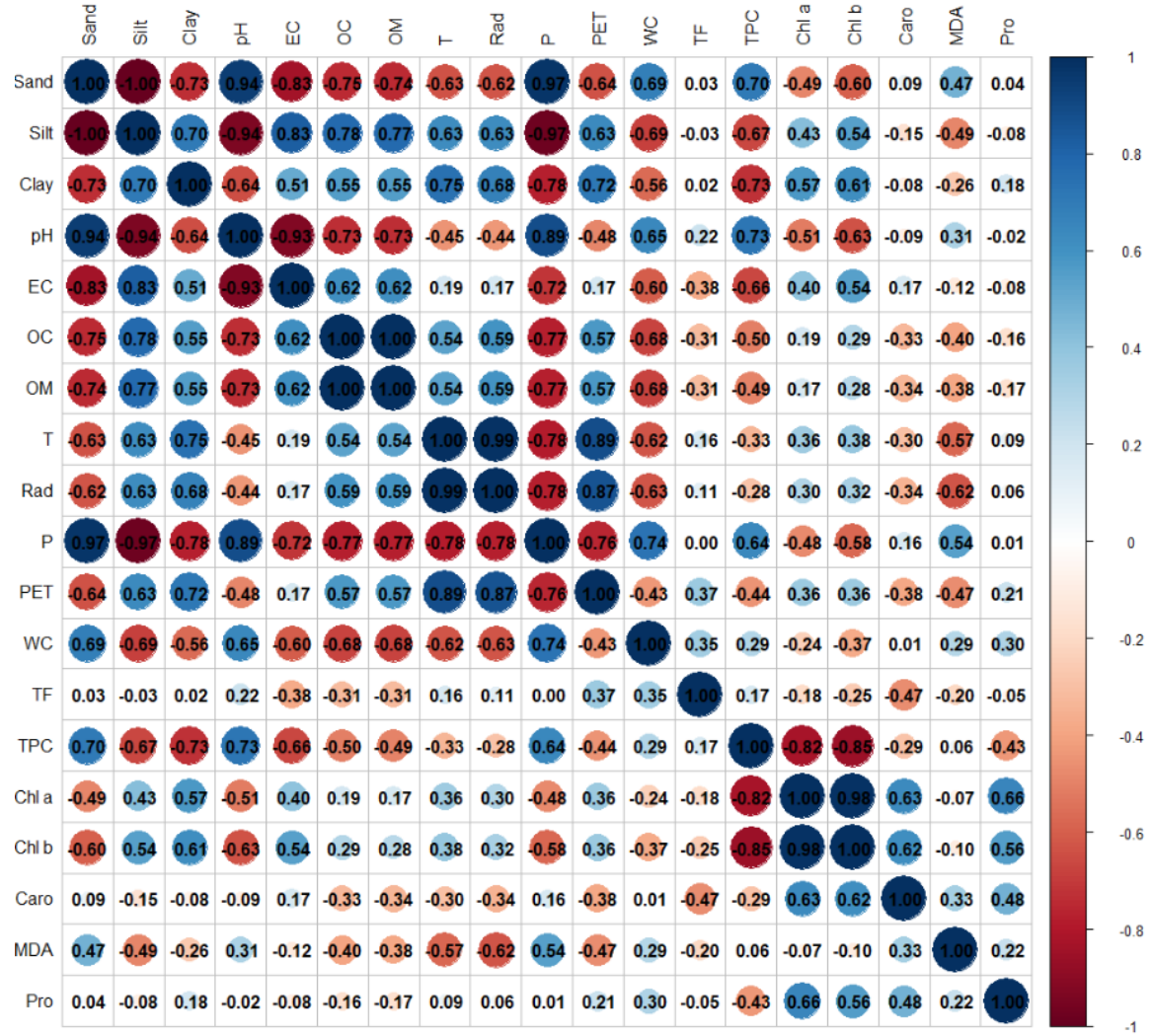

Figure 4. Scatter plot showing the pairwise Spearman's correlation coefficients calculated for the 19 traits analysed in 11 wild populations of *S. fruticosa* from the Valencian Community region in E Spain. Abbreviations as in Table 5.

4. Discussion

The study area includes 11 natural populations of *S. fruticosa* in eastern Spain, from the province of Castellón in the north to Valencia and Alicante in the south of this territory. All these regions experience a thermo-Mediterranean climate, with notable variations in

the annual rainfall. Specifically, some northern localities received almost twice as much precipitation in the period analysed as the southernmost areas.

The soil samples varied in textural class from sandy to silty, none with more than 10% clay. The predominant textural class in the soil samples obtained is silt loam, followed by sandy texture and silt loam, and only one was silt. Although the edaphic conditions varied considerably, from sandy to clayey soils and with different levels of electrical conductivity, the plant exhibited a remarkable ability to prosper in these diverse environments. According to the data obtained, all the soil samples analysed can be considered very saline or extremely saline. Their formation is generally due to a lack of drainage and a high percentage of evaporation, which causes the accumulation of salts. All soil samples showed a high content of organic matter. Despite the edaphic heterogeneity, *S. fruticosa* was well represented in all locations, forming almost monospecific communities that were poor in species diversity, as is typical for *Sarcocornia* species [33]. A previous study performed on La Mata lagoon, near the TV population analysed here, indicated that the species C, Koch, together with *Arthrocnemum macrostachyum* (Moric.), predominated in the most saline areas, on loam and silty–loam textures soils [34]. Its high tolerance to salinity was reported in numerous studies under controlled greenhouse conditions [8,35–37]. *Sarcocornia fruticosa* seeds are able to germinate under hypersaline conditions [38], and optimal growth was reported under irrigation with 510 mM NaCl solution [8]. The species was also reported as tolerant to metal and heavy metal-contaminated soils and, therefore, recommended for phytoremediation [39,40].

Due to their exceptional salt tolerance, species of the genera *Sarcocornia* and *Salicornia* are considered promising candidates for saline agriculture. Research on the potential use of halophytes as crops is increasing in parallel with the limitation of freshwater resources and rising soil salinity worldwide [41]. Plants living in harsh environments, such as saline or arid areas, synthesise, in response to abiotic stressors, a wide range of metabolites, some of which are of special interest with regard to human health [42,43]. These species have a nutritional profile recommended for the human diet, with high levels of proteins and fatty acids, particularly linoleic acids, sugars, alcohols, quaternary amino acid derivatives, tertiary amines, and sulphonic compounds, with low concentrations of toxic elements [44–46]. Of particular interest are the secondary metabolites synthesised by plants to prevent oxidative stress associated with salinity, such as phenolic compounds and vitamins, which make halophytes a food source with functional properties [21]. The nutritional value of various *Sarcocornia* species has been compared with commonly consumed green vegetables like lettuce (*Lactuca sativa*). This comparison highlights the potential of *Sarcocornia* in human nutrition, focusing on its proximate composition and bioactive compounds, suggesting that *Sarcocornia* could be a valuable dietary addition, especially in areas where it naturally grows [17].

In the present study, several compounds with antioxidant properties were investigated, such as carotenoids (analysed together with chlorophylls *a* and *b*), phenolic compounds, flavonoids, proline and MDA, as a marker of oxidative stress. Carotenoids are a large group of photosynthetic pigments that play an essential role in protection against photooxidative damage and as precursors of phytohormones. They are important in the human diet for their antioxidant properties and for acting as a source of β-carotene, which is the precursor of provitamin A [47]. The amount of chlorophylls provides a measure of the green colour of vegetables and is often used by customers as an indicator of vegetable senescence, although it is not particularly essential in terms of nutritional profile [41]. Although there were large differences in soil salinity at the sampling sites, no significant variations in chlorophyll *a*, *b* and carotenoid concentrations were found. When plants of this species were subjected to increasing salt stress under greenhouse conditions, photosynthetic pigments were not affected by salinity, drought or in post-stress recovery treatments [36,37], but there are also reports of a gradual increase in carotenoids in parallel with salt concentration [35].

Oxidative stress, or the overproduction of reactive oxygen species (ROS), is linked to abiotic stress. ROS are now recognised to have a critical function as signalling messengers

in various important physiological processes, contrary to the previous belief that they were simply harmful byproducts of aerial metabolism that lead to oxidative stress [48]. Excess ROS can damage lipids, proteins and nucleic acids, which can result in major dysfunctions and, eventually, cell death [49]. Membrane permeability and selectivity are changed by lipid peroxidation, which is caused by various ROS [50]. A byproduct of unsaturated fatty acid peroxidation is malondialdehyde (MDA), which is frequently employed as a marker of free radical damage to plant and animal cell membranes [51,52]. However, due to methodological flaws or incorrect interpretation of the data, its validity as a measure of oxidative stress has recently come under scrutiny [53]. Two of the communities studied, C1 and C2, had substantially lower MDA concentrations. Despite living in the same region of Alicante, their salinities varied greatly, making it difficult to explain the pattern of MDA variation. Previous reports on this species are also contradictory, ranging from an increase under salt concentrations of up to 600 mM NaCl [35] to no variation under salt treatments but a significant increase in plants sampled after recovery [36].

Excessive ROS accumulation in plants is prevented by the activation of defence systems, including synthesis of antioxidant metabolites like glutathione, carotenoids, flavonoids, phenols, or tocopherols and antioxidant enzymes, such as superoxide dismutase (SOD), catalase (CAT), ascorbate peroxidase (APx) (and other peroxidases), or glutathione reductase (GR) [49]. Antioxidant enzymes are considered the primary ROS-scavenging system involved in the first response to oxidative stress, whereas non-enzymatic antioxidants represent a secondary line of defence against oxidative stress, becoming active only under severe stress conditions when the activation of antioxidant enzymes is not sufficient to counteract the damaging effects of ROS [54].

Phenolic compounds, and especially flavonoids, represent an important antioxidant defence mechanism, playing important biological roles in plants and exhibiting biological properties potentially associated with multiple health benefits [55]. Although ubiquitous in plants, they are more frequent in certain taxonomic or functional groups. *Sarcocornia* species were reported to have high phenolic and flavonoid contents, but their concentration can vary between species, ecotypes or the extraction procedure [17].

Although many halophytes have been documented to exhibit increased phenolic and flavonoid concentrations in response to stress [50,56–58], no appreciable variation has been observed in many others [55,56]. Since the more salt-tolerant species have effective ways of controlling the creation of excessive ROS, such as reducing the amount of Na^+ that accumulates in the cytosol, it is very likely that they do not require the activation of antioxidant systems [59]. In this study, we detected significant differences in phenolic and flavonoid concentrations among the populations analysed, but these differences were not correlated with environmental stress factors, such as salinity or drought. This finding is in agreement with results previously reported in one of the areas included in this study (MM) where the levels of MDA or enzymatic and non-enzymatic antioxidants in five halophyte species (including *S. fruticosa*) sampled during two years in different seasons were not correlated with the degree of environmental stress [60]. On the contrary, a similar study performed in two coastal areas of Egypt found a significantly higher content of phenolics and flavonoids in the dry season (July 2017) than in the wet season (March 2018) [61]. Different accumulation patterns of these compounds were also found in greenhouse experiments, with some reports indicating no variation under saline treatments or in recovery after stress [36], and even a decrease in their concentrations with increasing salinity [35], but also higher concentrations in plants from saline treatments with respect to the control [46].

Proline is one of the most common osmolytes in plants [62]. Apart from its function as a compatible solute, Pro acts as a potent antioxidant, directly quenching ROS or stabilising ROS-scavenging and mitochondrial respiration enzymes [62]. *S. fruticose*, like other species of this genus, is not a proline accumulator, its main osmolyte being glycine betaine [36,60]. The proline concentrations in all samples were low, similar to those previously reported in this species, but proline could enhance the stress tolerance of plants by its ability to

scavenge ROS, directly stabilise proteins and other cellular structures and provide cellular redox potential.

Despite variations in soil and climatic factors, the levels of biochemical compounds in the different populations of *S. fruticosa* did not show a clear correlation with environmental conditions. The concentrations of antioxidant compounds, such as phenols, flavonoids, and proline, as well as MDA, did not follow a specific pattern related to salinity or precipitation. This suggests that the differences in the levels of these compounds between populations are likely of genetic origin rather than a direct adaptive response to environmental conditions.

Principal Component Analysis was chosen as a versatile method of linear dimensionality reduction used to visualise the clusters in a dataset, to identify outliers, or to visualise the relationships between variables [63]. Nonetheless, neither this method nor the Spearman correlations applied have been able to detect a clear and logical pattern between plant variables and climatic and soil data. The level of succulence was higher in plants from areas with higher rainfall, but no correlations have been observed with the concentrations of biochemical compounds, nor has a clear pattern been observed between the concentrations of antioxidant compounds or MDA and salinity.

This study supports the potential of *S. fruticosa* as a promising halophyte species for agriculture in saline soils. Its ability to thrive in a variety of edaphic and climatic conditions, along with its antioxidant profile, underlines its potential value for applications in biosaline agriculture and saline soil rehabilitation. Chemical antioxidants, such as phenols and, in particular, flavonoids, play an important role in the stress tolerance of plants but, at the same time, are responsible for the quality of vegetables [64]. Due to their wide range of biochemical and pharmacological activities, antioxidants are considered as health-promoting and disease-preventing dietary supplements [65].

The lack of a clear correlation between biochemical compounds and environmental conditions highlights the need for further studies to better understand the genetic and metabolic mechanisms that may influence antioxidant production in *S. fruticosa*. Differences in the responses of antioxidant systems between populations have been reported in several halophytes [66–68], but analysis of the genetic variability of populations in combination with quantification of antioxidants have been performed only in crops [69,70] or wild species with an economic interest [71] and, to the best of our knowledge, not in halophytes. The results obtained suggest that the concentration of antioxidants produced by the plants will not increase when watered with a higher concentration of NaCl, and, therefore, irrigation should be at the optimum NaCl concentration for the growth of this species. However, of considerable interest is also testing the in vitro antioxidant capacity of plants from different populations by different methods [72], such as DPPH (free radical 2,2-Diphenyl-1-picrylhydrazyl) or FRAP (ferric reducing antioxidant power assay). Future research could also focus on identifying the genetic factors responsible for the observed biochemical variability and assessing *S. fruticosa*'s suitability for agriculture under various salinity and environmental stress conditions.

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