Agriculture and Food

AIMS Agriculture and Food, 9(3): 716–742.
DOI: 10.3934/agrfood.2024039
Received: 05 March 2024
Revised: 09 May 2024
Accepted: 24 May 2024
Published: 21 June 2024

https://www.aimspress.com/journal/agriculture

Research article

Determination of bioactive compounds and antioxidant capacity of the halophytes *Suaeda edulis* and *Suaeda esteroa* (Chenopodiaceae): An option as novel healthy agro-foods

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Abstract: Food security is relevant due to the uncertain availability of healthy food. Accordingly, it is necessary to know the biological potential of new crops as a food source to meet the basic nutritional

needs of a growing population. This study aimed to analyze chemical extractions of the cultivated species *Suaeda edulis* and its wild relative *S. esteroa* to determine their biological and nutritional value. For analysis, we collected 25 plants of *S. edulis* in the chinampas-producing area of Xochimilco, Mexico City, and 25 plants of *S. esteroa* in Balandra beach, Baja California Sur, Mexico. We quantified total phenols, total flavonoids, and the total antioxidant capacity of free and conjugated fractions by Folin-Ciocalteu, aluminum trichloride, DPPH, and TEAC spectrophotometric methods. *S. esteroa* reflected a higher content of total phenols, total flavonoids, and total antioxidant capacity (free and conjugated) than the values of *S. edulis*. We determined 39.94 and 49.64% higher values of total phenol content in *S. esteroa* than *S. edulis*, 36 and 40.33% in total flavonoid content, 32.92 and 40.50% in total antioxidant capacity by DPPH, and 34.45 and 48.91% by TEAC for free and conjugated fractions, respectively. We identified 11 phenolic compounds in both halophytes; among them, the free form ferulic acid, gallic acid, and rutin showed high concentrations in *S. edulis*, whereas quercetin and ferulic acid were more abundant in *S. esteroa*. The conjugated fraction showed lower concentrations than the free fraction. In conclusion, we found a high biologically active potential of the halophytes studied; this could boost their consumption, which in turn would offer *S. edulis* and *S. esteroa* as new sustainable crops to help address food shortages in regions with water scarcity or soil salinity, as well as to counteract chronic degenerative diseases associated with obesity.

Keywords: halophytes; new crops; phenols; flavonoids; antioxidants; *S. edulis*; *S. esteroa*

1. Introduction

Weight excess and obesity are conditions that have reached epidemic proportions worldwide [1]. During obesity, chronic low-grade inflammatory processes, insulin resistance, metabolic dysfunction, hormonal alterations, oxidative stress, epigenetic changes, and alterations in the gut microbiome can be observed [2–5]. These conditions can promote chronic degenerative diseases such as diabetes, hypertension, cardiovascular diseases, and some types of cancer [6]. Relevant lifestyle changes are necessary for preventing these diseases; however, anti-inflammatory drugs and those that improve insulin sensitivity have also been effective [7,8]. On the other hand, therapies that aid in hormonal modulation, epigenetic changes, and the modulation of the gut- microbiome have been investigated [9–11]. Another relevant mechanism to counteract these conditions is the consumption of foods with a significant content of phenolic compounds that, due to their chemical structure such as functional groups, number of hydroxyl groups, and conjugation of double bonds, have antioxidant effects [12] that help in the reduction of oxidative stress, DNA protection, preservation of cell membranes, inhibition of inflammation, and protection of the cardiovascular system [13].

Due to the potential phenolic compounds have in diet [14], a search for new sources of these has been ongoing [15], including the use of microorganisms such as bacteria and fungi [16,17], agricultural by-products [18,19], microalgae [20], cereals [21,22], and the use of non-conventional plants [23,24]. Among the unconventional plant species are the named halophytes, adapted plants that can fulfill their entire life cycle at levels $\geqslant$ 200 mM NaCl [25–27]. In addition to the saline conditions in which halophytes grow, they suffer from various types of abiotic stress, such as high levels of ultraviolet light, soil acidification, and pollutants such as microplastics, heavy metals, and pesticides [28]. The presence of these conditions leads to increased oxidative stress in plants and the synthesis of reactive oxygen

species (ROS), which in turn can cause damage to proteins, lipids, and DNA, as well as imbalance in cell homeostasis, cell division, and growth, and cell organelle dysfunction [29–31].

Adverse environmental conditions induce the acquisition of distinctive characteristics in halophytes, manifesting in both their anatomy and morphology, as well as in the implementation of physiological mechanisms. These include the capacity for salt accumulation or exclusion, ionic compartmentalization, osmotic adjustment, and the synthesis of phenolic compounds. These compounds play a crucial role in the mitigation of oxidative stress in plants, protection of proteins and enzymes, reduction of DNA damage, modulation of the cell cycle, and stimulation of defense mechanisms [32–34]. Accordingly, there is a proven accumulation of these compounds in halophyte plants, confirmed in studies with *Limonium effusum, L. sinuatum, Spergularia marina* (L.) Griseb., and *Glaux maritima* L. with significant amounts of phenolic compounds such as gallic acid, p-Coumaric acid, 4-hydroxybenzoic acid, trans-caffeic acid, protocatechuic acid, and kaempferol, among others [35,36]. Several studies have shown that, due to the presence of these bioactive compounds, effects on enzyme and gene inhibition can be observed in various models, proving potential anticancer [37], antidiabetic [38], and antihypertensive [39] effects from their consumption.

Determining the bioactive potential of the halophytes *Suaeda edulis* and *S. esteroa* will boost their consumption as food, offering new sustainable crops as a viable option to address food shortages in regions with water scarcity or soil salinity, as well as to counteract chronic degenerative diseases associated with obesity.

2. Materials and methods

2.1. Study site and experimental setup

2.1.1. Soil and climate of collecting regions

The predominant climate in Xochimilco, where *S. edulis* grows, is C (W2) (w) b (i′) (Köppen climate classification system with modifications); the rainy season is in summer, between May and October, with an average annual historical rainfall of 620.4 mm. The annual mean temperature ranges between 12 and 18 °C. Frosts occur between November and January [40,41]. In Balandra beach (Baja California Sur), where the wild species *S. esteroa* grows, the predominant climate is warm and semi-dry, with high daytime temperatures and dryness. The annual historical precipitation is scarce, ranging from 120 mm in the north to 310 mm in the south; dry periods occur in winter and spring. In summer, the minimum temperature ranges from 5 to 12 °C, and the maximum temperature exceeds 40 °C [42].

The presence of clay soil types due to the mineral accumulation process characterizes the growing region of Xochimilco, reflecting physical and chemical alteration of alluvial materials and volcanic ashes in a lacustrine environment forming the Chinampas. Along the edaphic sequence, the interstitial fluids are composed of different concentrations of cations such as calcium, magnesium, sodium, and potassium, with the production of soluble ions leading to salt increases in the soil from 5 up to 40 meq/100 g soil. A negative effect of the salt increase on the top layer of the soil is reducing the agricultural capacity of the Chinampera zone of Xochimilco [43]. On the other hand, the soils of Balandra beach are mainly silty and sandy soils; they often receive high volumes of saline water from tides. Due to the dynamics of tide arrivals, the eventual accumulation of sediments and organic matter occurs [44].

2.1.2. Experimental setup

The Functional Food Laboratory of the Research Department and Postgraduate in Food (DIPA) supported this study with equipment and guidance for the experimental setup and analysis. This Lab belongs to the University of Sonora (UNISON), Campus Centro, located in the City of Hermosillo, Sonora, in Northwest Mexico.

2.2. Sampling locality geographical information

For the laboratory analysis, we collected plants in the medium growth stage with vigorous appearance and without symptoms of biotic damage. For this, by random sampling we collected a sample of 25 plants of *S. edulis* in the chinampa production area of the municipality of Xochimilco, located in the southwest of Mexico City (19.2769° N, 99.1110° W), and 25 plants of *S. esteroa* in Balandra beach, 8 km west La Paz city, Baja California Sur, Mexico (24°18′44″ N, 110°19′44″ W). We carried out sampling with pruning shears and cutting stems and leaves. The collection period for both species was in December 2021 (Figure 1).

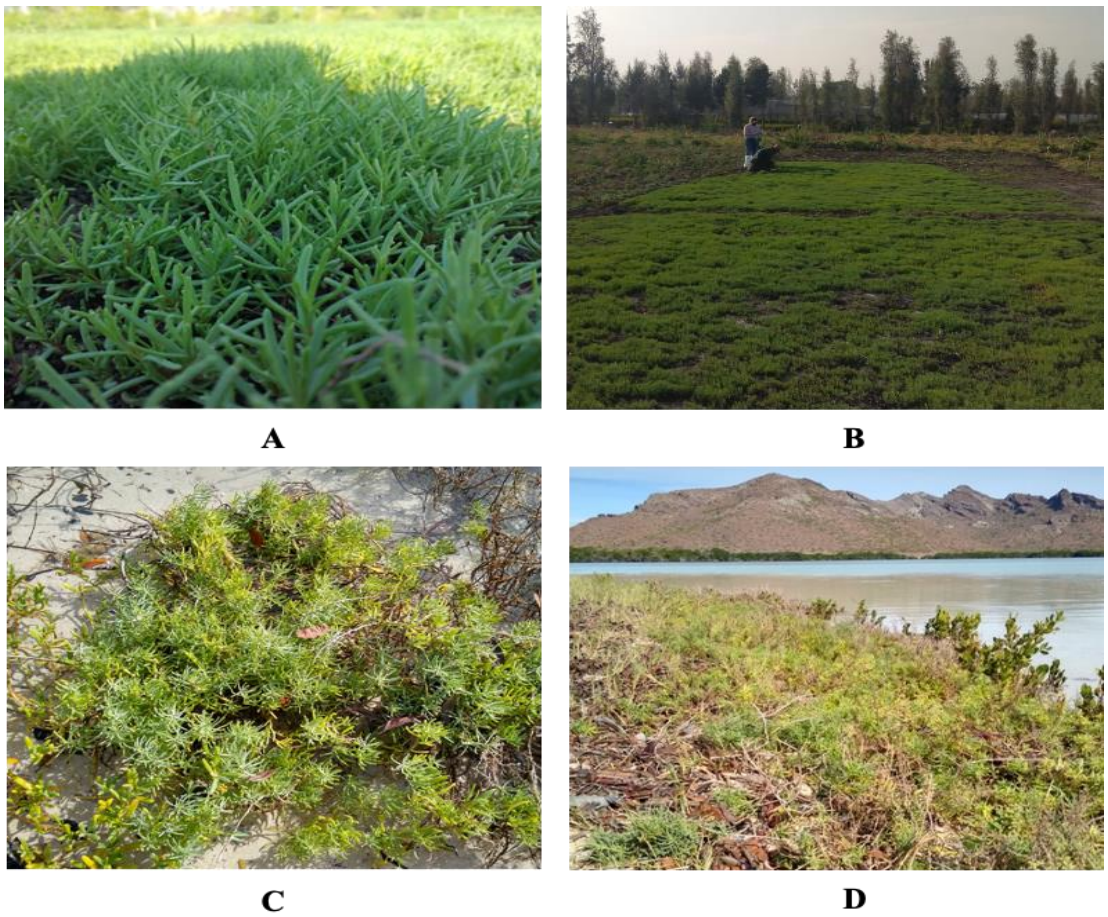

Figure 1. Plants of *S. edulis* and *S. esteroa* in their natural habitats; (A, B) *S. edulis* in the production region of Xochimilco, Mexico City, and (C, D) *S. esteroa* in the wild coastal area of Balandra beach, La Paz, Baja California Sur, Mexico.

2.3. Biomass processing and flour production methods

First, to remove the surface residues from the field, *S. edulis* and *S. esteroa* plants were rinsed with distilled water, dried, and stored in 26.8 x 27.27 cm Ziploc® plastic bags for freezing, then were frozen at −70 °C in a Thermo Scientific Revco Value Series ultra-freezer for 1-h. Subsequently, we lyophilized them at −50 °C in a LabConco® FreeZone® Freeze Dry System for three days. Later, freeze-dried plants were ground and pulverized in a mill SV-MO-100T, obtaining flours with a particle size < 0.45 mm (Figure 2).

A B

Figure 2. Flours obtained from freeze-dried biomass from *S. edulis* (A) and *S. esteroa* (B).

2.4. Extraction of free compounds

Free-form phenolics are directly released and easily detected, while the conjugated and bound forms must be alkaline hydrolyzed before being perceived during processing or storage. To allow solubilization of the free compounds present in the samples of both species, the methanolic extracts obtention followed the procedure described by Salazar-López et al. [45]. First, 1 g of each flour was weighed into the 13 mL Pyrex® test tubes with a digital analytical balance Sartorius TE124S, adding 13 mL 80% methanol (MeOH). The formed suspensions were homogenized in a VELP® Scientifica vortexer at 35 rpm, sonicated for 1-h in a Branson 2510 sonicator at 30 °C, and centrifuged in a Velaquin Civeq 80-2 centrifuge at 4000 rpm for 15 min. The supernatants obtained through phase separation (liquid-solid) were filtered with Whatman n°1 filter paper and collected in a 50 mL Falcon tube. Posteriorly, extraction of solid residues was under the same conditions, but adding some 30 min each. Next, the supernatants were evaporated to dryness in an R-100 Buch Switzerland vacuum rotary evaporator at 40 °C and resuspended in 7 mL of 50% methanol. The obtention of the methanolic extracts was at a concentration of 0.1428 g/mL.

2.5. Extraction of conjugated compounds

The interaction between proteins and polyphenols, yielding 'protein-polyphenol conjugate', spontaneously occurs in most food systems; this is the reason for applying different analytical methods for free and conjugated compounds [46]. To favor solubilizing the conjugated compounds present in the samples of *S. edulis* and *S. esteroa*, the alkaline extracts, we followed the procedure described by Adom and Liu [47]. First, 1 mL of each fraction of free phenolic compounds obtained from the methanolic extraction was taken in glass vials, adding 5 mL of degassed 2 M sodium hydroxide (NaOH). Next, the air was displaced with nitrogen (N_2) for 30 sec in an OA-System heating-evaporator and sonicated for 1 h in a Branson 2510 sonicator at 30 °C. The pH was then adjusted to 1.5–2.0 with 6 M hydrochloric acid (HCl) and 2 M sodium hydroxide (NaOH) in a Hanna 211 digital pH meter, then adding approximately 7 mL of ethyl acetate ($C_4H_8O_2$). The suspensions obtained were transferred to 13 mL Pyrex® test tubes and shaken manually for 2 min, obtaining the compounds released by the alkaline solution and by phase separation (liquid-liquid). They were then centrifuged in a Velaquin CIVEQ 80-2 centrifuge at 4000 rpm for 15 min and collected in a 50 mL Falcon tube. Later, the extraction of the other fraction of the phase was under the same conditions but extending 15 more min each. Next, the supernatants were evaporated to dryness in an R-100 Buch Switzerland vacuum rotary evaporator at 40°C and resuspended in 5 mL of 50% methanol, obtaining the alkaline extracts at 0.028 g/mL concentration.

2.6. Determination of total phenolic compounds

The content of free and conjugated total phenols compounds of *S. edulis*, and *S. esteroa* extracts was quantified spectrophotometrically by the colorimetric method using Folin-Ciocalteu reagent (FCR), as described by Salazar-López et al. [45]. Briefly, we prepared the following: (1) The Folin's reagent (1:9) and (2) sodium carbonate (Na_2CO_3) (0.075 mg/mL), both diluted in distilled water. Posteriorly, 30 µL of each extract was mixed with 150 µL of Folin's reagent and 120 µL of sodium carbonate using a NuncTM Edge multiwell plate. The mixture was homogenized and allowed to stand to react in the dark for 1 h. Next, changes in the absorbance were determined at 765 nm using a spectrophotometer-microplate reader FluoStar Omega BMG Labtech Inc., Ortenberg, Germany. Results were expressed in mg of gallic acid equivalents per gram of the sample (mg GAE/g), using a curve as a reference standard.

2.7. Determination of total flavonoid compounds

The content of free and conjugated total flavonoid compounds of *S. edulis* and *S. esteroa* extracts was quantified spectrophotometrically by the colorimetric method using aluminum trichloride, as described by Valenzuela-González et al. [48]. For this purpose, we prepared the following solutions: (1) Sodium nitrite ($NaNO_2$) (0.05 mg/mL), (2) aluminum trichloride ($AlCl_3$) (0.1 mg/mL), and (3) sodium hydroxide (NaOH) (0.04 mg/mL), each diluted in distilled water. Posteriorly, using a NuncTM Edge multiwell plate, 30 µL of each extract was mixed with 9 µL of sodium nitrite and 120 µL of distilled water and allowed to stand for 5 min. Next, 9 µL of aluminum trichloride was added and left to stand for another 5 min, adding finally 60 µL of sodium hydroxide and 72 µL of distilled water, shaking the mixture in a microplate reader. Next, changes in the absorbance were determined at 415

nm using a spectrophotometer-microplate reader FluoStar Omega BMG Labtech Inc., Ortenberg, Germany. Results were expressed in mg of quercetin equivalents per gram of the sample (mg QE/g), using a curve as a reference standard.

2.8. Determination of antioxidant capacity

2.8.1. DPPH ´2,2-Diphenyl-1-picrylhydrazyl´ assay

The spectrophotometric assay of the antioxidant capacity by DPPH (2,2-Diphenyl-1-picrylhydrazyl) of the free and conjugated total compounds of *S. edulis* and *S. esteroa* followed the procedure described by Ruiz-Hernández et al. [49]. Then, we prepared the working radical solution immediately before its use by mixing 2.5 mg of DPPH with 100 mL of methanol (MeOH). The obtained solution reflected an intense purple color, which was adjusted to an absorbance of 0.7 ± 0.02 at a wavelength of 515 nm using a spectrophotometer-microplate reader FluoStar Omega BMG Labtech Inc., Ortenberg, Germany. Posteriorly, 20 µL of each extract was mixed with 280 µL of reagent (DPPH radical) using a NuncTM Edge multiwell plate. The mixture was homogenized and allowed to stand to react in the dark for 1 h, then registering the absorbance changes at the same wavelength with the same microplate reader. Results were expressed in µmol of Trolox equivalents per gram of the sample (µmol TE/g), using a curve as a reference standard.

2.8.2. TEAC ´Trolox Equivalent Antioxidant Capacity´ assay

The spectrophotometric assay of the antioxidant capacity by TEAC equivalent in Trolox '6-hydroxy-2,5,7,8-tetramethylchroman-2-carboxylic acid (in English: Trolox Equivalent Antioxidant Capacity) of the free and conjugated total compounds of *S. edulis* and *S. esteroa* followed the procedure described by Salazar-López et al. [50]. Briefly, the ABTS radical activating stock solution was prepared, including the following solutions: (1) ABTS ('2,2'-azinobis [3-ethylbenzothiazoline-6-sulphonic acid]-diammonium salt) (19.3 mg/mL) and (2) potassium persulfate ($K_2S_2O_8$) (37.8 mg/mL), both diluted in distilled water. 88 µL of the solution (2) was taken and added to solution 1. The obtained solution reflected an intense blue color, which was allowed to stand for 16–18 h in the dark at room temperature. Posteriorly, the working solution of the radical was prepared immediately before use by mixing 1.5 mL of the stock solution with 100 mL of ethanol (C_2H_6O); the solution obtained reflected a less intense blue color, which was adjusted to an absorbance of 0.7 ± 0.02 at a wavelength of 734 nm using a spectrophotometer-microplate reader FluoStar Omega BMG Labtech Inc., Ortenberg, Germany. Later, we mixed 20 µL of each extract with 280 µL of reagent (ABTS radical). The mixture was homogenized and allowed to stand to react in the dark for 5 min. Next, absorbance changes at the same wavelength were then determined using the mentioned microplate reader. Results were expressed in µmol of Trolox equivalents per gram of the sample (µmol TE/g), using a curve as a reference standard.

2.9. Quantification of total phenols and flavonoids by Ultra High-Performance Liquid Chromatography (UHPLC) equipped with a Diode Array Detector (DAD)

The quantification of free and conjugated compounds of total phenols and flavonoids of *S. edulis* and *S. esteroa* followed the procedure described by Lee et al. [51] with slight modifications, using the

Ultra High-Performance Liquid Chromatography (UHPLC) system from Agilent Technologies 1260, Germany, equipped with a Diode Array Detector (DAD). Then, we used a Zorbax Eclipse Plus-C18 reversed-phase column (2.0 mm x 50 mm 1.8 microns) at 30°C for detecting five phenolic acids and six flavonoids. A two-phase mobile binary elution system of (A) water:formic acid (99.9:0.1) and (B) acetonitrile:formic acid (99.9:0.1) was applied. For this, we applied the following linear elution gradient.

0–3 min (phase A: 97-93% and phase B: 3-7%); 3–5 min (phase A: 93-90% and phase B: 7-10%); 5–8 min (phase A: 90-88% and phase B: 10-12%); 8–10 min (phase A: 88-85%, and phase B: 12-15%); 10–15 min (phase A: 85-85%, and phase B: 15-15%); 15–18 min (phase A: 85-45%, and phase B: 15-55%), and 18–20 min (phase A: 45-10%, and phase B: 55-90%). The flow rate was 0.4 mL/min, and the injection volume was 5 µL. To identify the phenol and flavonoid compounds, we prepared the required aqueous methanol extracts by comparing retention time and peaks of the UV spectra of the samples with those of pure reference standards. The results were expressed as µg of phenol acids and flavonoids per gram (µg phenol ac and flav/g) of the sample, using reference curves with each of the acids at different concentrations.

2.10. Data collection and statistical analysis

For numerical analysis, the data of the variables under study were tabulated and classified in spreadsheets (Excel® 365 version 2022). Results were analyzed with parametric statistical methods, using the Kolmogorov-Smirnov normality test [52] and Levene's similarity of variances test [53] to verify the data normal distribution, except for the quantification of the phenol and flavonoid compounds determined by UHPLC-DAD, since statistical programs require at least five data to perform statistical tests and, in this case, we have three data for each variable. We compared the differences between species with the t-Student test at a 95% significance level ($p < 0.05$), generating statistical graphs with the free statistical software PAST version 4.10 [54].

3. Results and discussion

The statistics for the normality (Kolmogorov Smirnov test) and homoscedasticity (Levene´s test) were favorable for applying the statistical parametric analyses, except in five of the twenty-four cases in which the test for equality of variances did not detect similarity. Despite these different cases, and because most met assumptions of normality and homoscedasticity, it was possible to continue with the Student's t-test and the comparison of means (Tables 1 and 2).

3.1. Free and conjugated total phenolic compounds

Phenolic compounds in plants can be found in different forms, occupying a specific function according to their location [55,56]; among these, the antioxidant effects [57] to face the ROS caused by different types of biotic or abiotic stresses [58,59] stand out. This effect is also relevant when a diversity of plants is part of conventional and novel diets, where the compounds of the free fraction could more easily exert a beneficial effect on the consumer. On the other hand, those bound compounds will be subject to hydrolysis, which may or may not exert a beneficial effect if this is carried out during their digestion [60,61]. In the analyzed plants, *S. esteroa* is 39.94% higher in the content of phenolic

compounds in the free fraction when compared to *S. edulis* (3.83 and 2.30 mg GAE/g). On the other hand, the conjugated fraction reflected similar results, where *S. esteroa* presented 49.64% more phenolic compounds compared to *S. edulis* (1.41 and 0.71 mg GAE/g), showing highly significant differences between species ($p < 0.001$) (Figure 3).

Table 1. Normality test for free and conjugated total phenols, flavonoids, and antioxidant capacity DPPH and TEAC of *S. edulis* and *S. esteroa*.

Species	Statistic D	p-Value	Significance
Free total phenols (mg GAE/g, dw)			
S. edulis	0.15698	0.70977 ^{ns}	Does not differ from normal distribution
S. esteroa	0.20713	0.37106 ^{ns}	
Conjugated total phenols (mg GAE/g, dw)			
S. edulis	0.21261	0.34055 ^{ns}	Does not differ from normal distribution
S. esteroa	0.21874	0.30841 ^{ns}	
Free total flavonoids (mg QE/g, dw)			
S. edulis	0.16211	0.67293 ^{ns}	Does not differ from normal distribution
S. esteroa	0.17655	0.56922 ^{ns}	
Conjugated total flavonoids (mg QE/g, dw)			
S. edulis	0.2221	0.29172 ^{ns}	Does not differ from normal distribution
S. esteroa	0.13346	0.86459 ^{ns}	
Free total antioxidant capacity DPPH (µmol TE/g, dw)			
S. edulis	0.14078	0.82037 ^{ns}	Does not differ from normal distribution
S. esteroa	0.187	0.49692 ^{ns}	
Conjugated total antioxidant capacity DPPH (µmol TE/g, dw)			
S. edulis	0.19873	0.42102 ^{ns}	Does not differ from normal distribution
S. esteroa	0.20741	0.36946 ^{ns}	
Free total antioxidant capacity TEAC (µmol TE/g, dw)			
S. edulis	0.15886	0.69633 ^{ns}	Does not differ from normal distribution
S. esteroa	0.26829	0.12371 ^{ns}	
Conjugated total antioxidant capacity TEAC (µmol TE/g, dw)			
S. edulis	0.14361	0.80208 ^{ns}	Does not differ from normal distribution
S. esteroa	0.13623	0.84842 ^{ns}	

Notes: mg GAE/g, dw (mg of gallic acid equivalents/g of sample, dry weight); mg QE/g, dw (milligrams of quercetin equivalents/g of sample, dry weight); DPPH (2,2-Diphenyl-1-picrylhydrazyl); TEAC (Trolox Equivalent Antioxidant Capacity); µmol TE/g, dw (micromoles of Trolox equivalents/g of sample, dry weight); non-significant p's ($p > 0.05$) are indicated with (^{ns}).

Table 2. Homoscedasticity test for free and conjugated total phenols, flavonoids, and antioxidant capacity by DPPH and TEAC of *S. edulis* and *S. esteroa*.

Species	Statistic F	p-Value	Significance
Free total phenols (mg GAE/g, dw)			
S. edulis and *S. esteroa*	4.7183	0.0369 *	Similarity of variances is not accepted
Conjugated total phenols (mg GAE/g, dw)			
S. edulis and *S. esteroa*	16.2312	0.0002 ***	Similarity of variances is not accepted
Free total flavonoids (mg QE/g, dw)			
S. edulis and *S. esteroa*	4.1945	0.0483 *	Similarity of variances is not accepted
Conjugated total flavonoids (mg QE/g, dw)			
S. edulis and *S. esteroa*	0.3860	0.5385 ns	Similarity of variances is accepted
Free total antioxidant capacity DPPH (µmol TE/g, dw)			
S. edulis and *S. esteroa*	6.0511	0.0191 *	Similarity of variances is not accepted
Conjugated total antioxidant capacity DPPH (µmol TE/g, dw)			
S. edulis and *S. esteroa*	1.4003	0.2448 ns	Similarity of variances is accepted
Free total antioxidant capacity TEAC (µmol TE/g, dw)			
S. edulis and *S. esteroa*	0.7286	0.3992 ns	Similarity of variances is accepted
Conjugated total antioxidant capacity TEAC (µmol TE/g, dw)			
S. edulis and *S. esteroa*	17.1516	0.0002 ***	Similarity of variances is not accepted

Notes: mg GAE/g, dw (mg of gallic acid equivalents/g of sample, dry weight); mg QE/g, dw (mg of quercetin equivalents/g of sample, dry weight); DPPH (2,2-Diphenyl-1-picrylhydrazyl); TEAC (Trolox Equivalent Antioxidant Capacity); µmol TE/g, dw (micromoles of Trolox equivalents/g of sample, dry weight); non-significant p's ($p > 0.05$) are indicated with (ns); significant $p \leq 0.05$ is indicated with (*); $p \leq 0.001$ is indicated with (***).

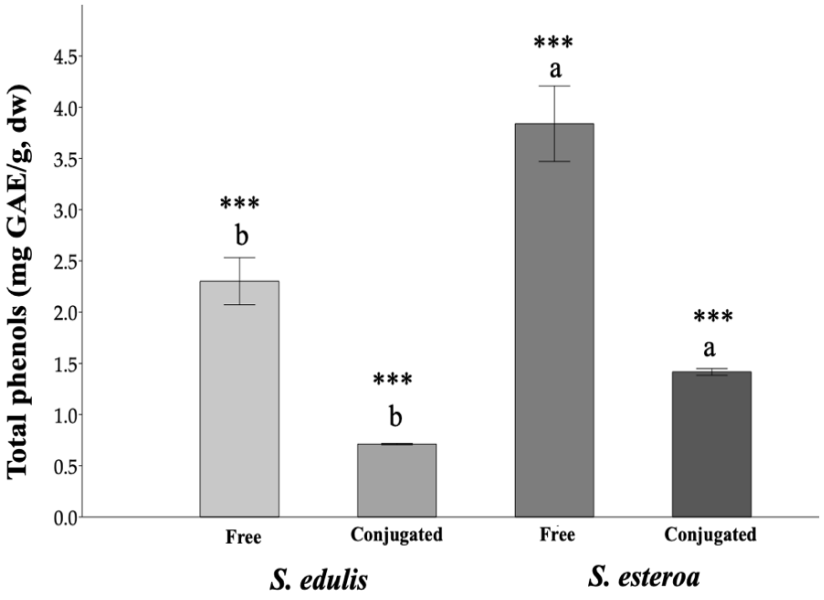

Figure 3. Free and conjugated total phenols (mg GAE/g, dw: dry weight) of methanolic and alkaline extracts of *S. edulis* and *S. esteroa*. Bars correspond to the mean ± standard deviation of three replicates. Superscripts a and b between bars indicate statistically significant differences between species (Student's t-test, $p \leq 0.001$).

According to the results, the differences in phenol content between the two plants may be due to the different growing conditions, where soil, climate, light, and other factors could significantly influence the content of phenolic compounds [62]. A previous study revealed that salinity induced evident changes in the amino acid composition and protein profiles of the principal seed storage proteins of quinoa, as well as in the contents of bioactive molecules; the antioxidant activity of seed protein extracts could be explained by the presence of phenolics [63]. In this sense, it is relevant to consider that, for the available extracts, the Folin-Ciocalteu technique can overestimate the reducing sugars or amino acids that are part of the plant matrix, so it would be necessary to investigate the compound to be obtained [64,65].

3.2. Free and conjugated total flavonoid compounds

Flavonoids differentiate and classify into different subgroups according to the degree of oxidation of the heterocyclic rings and the number of hydroxyl or methyl groups in the benzene ring [66]. Regarding their role in individuals and ecosystems, previous reports suggest that they can attract some classes of pollinating insects, also in cell growth, elimination of ROS, as signaling molecules, and help in heat tolerance, drought, and frost in several plant species [67,68]. *S. esteroa* in both fractions (free and conjugated) was found to account for more than 30% flavonoid content compared to *S. edulis*. Accordingly, *S. esteroa* is 36% higher in flavonoid content of the free fraction compared to *S. edulis* (5.25 and 3.36 mg QE/g); on the contrary, for the conjugated fraction samples of *S. esteroa* presented 40.33% higher flavonoid content compared to *S. edulis* (1.19 and 0.78 mg QE/g), showing highly significant differences between species ($p < 0.001$) (Figure 4).

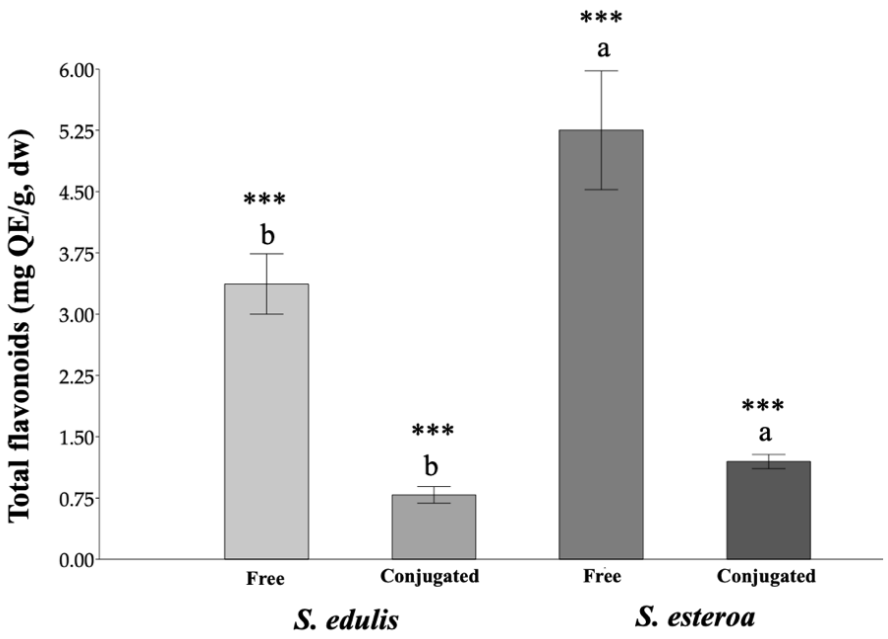

Figure 4. Free and conjugated total flavonoids (mg QE/g, dw: dry weight) of methanolic and alkaline extracts of *S. edulis* and *S. esteroa*. Bars indicate means ± std dev of three replicates. Superscripts a and b between bars indicate statistically significant differences between species ($p \leq 0.001$).

As discussed above, the differences among the studied halophytes on flavonoid content may be due to different growth conditions, thereby causing differences in their defense mechanisms, such as ionic homeostasis, ion uptake and transport, induction of osmoprotectants, and the activation and production of enzymes and antioxidant compounds [69]. However, although phenolic acids and flavonoids share some functions in plants, and flavonoids, in particular, can accumulate in the epidermis of leaves and other plant tissues to absorb UV radiation and thus protect the plant from damage caused by intense sunlight. Remarkably, phenolic acids are mainly involved in antioxidant functions that help neutralize free radicals generated during oxidative stress caused by stress [70].

3.3. Free and conjugated total antioxidant capacity by DPPH and TEAC

The antioxidant activity is widely studied in vegetable matrices and there is a diversity of species and varieties with different proportions of antioxidant components, while several techniques have been developed, including DPPH and TEAC methods. Giuffré [71] found that the correlation between the antioxidant activity of the bergamot juice measured with the DPPH assay was high with total flavonoid content ($r = 0.764$; $p < 0.001$). In another study, a positive correlation between antioxidant potency and total phenolic content indicated that phenolics could be one of the main contributors to the antioxidant capacities of fruit residues, especially the values of ferric-reducing antioxidant power (FRAP), Trolox equivalent antioxidant capacity (TEAC), and total phenols compounds (TPC), which were higher in residues than in pulps [72].

The content of phenols and flavonoids tends to correlate with the antioxidant activity; depending on the structure, the number of hydroxyl groups in the aromatic ring, its position, the presence of substituents, and the presence of double bonds reflect different activities [73]. Due to the above, in halophytes such as *Salsola dendroides* and *Limonium reniforme*, the antioxidant capacity is different, as well as the response to different seasonal conditions of the year, which would demonstrate the different response mechanisms that the plants present [74].

Therefore, regarding the antioxidant potential of DPPH in this study, *S. esteroa* reflected a higher antioxidant capacity than *S. edulis* in both fractions (free and conjugates). *S. esteroa* was 32.92 and 40.50% higher in its antioxidant capacity of the free (21.71 and 13.59 μmol ET/g) and conjugated (0.71 and 0.38 μmol ET/g) fractions, respectively, compared to *S. edulis*. Meanwhile, results with TEAC were similar, where *S. esteroa* was 34.45 and 48.91% higher than *S. edulis* in its antioxidant capacity of the free (26.79 and 17.56 μmol ET/g) and conjugated (0.92 and 0.47 μmol ET/g) fractions, respectively. Differences between species were highly significant ($p \leq 0.001$) (Figures 5 and 6).

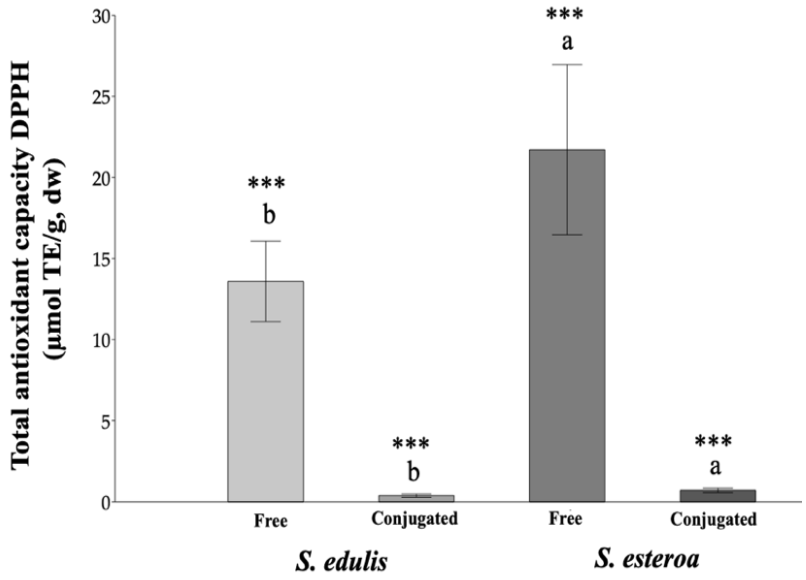

Figure 5. Total free and conjugated antioxidant capacity by DPPH (µmol ET/g, dw: dry weight) of methanolic and alkaline extracts of *S. edulis* and *S. esteroa*. Bars correspond to the mean ± standard deviation of three replicates. Superscripts a and b between bars indicate statistically significant differences between species ($p \leq 0.001$).

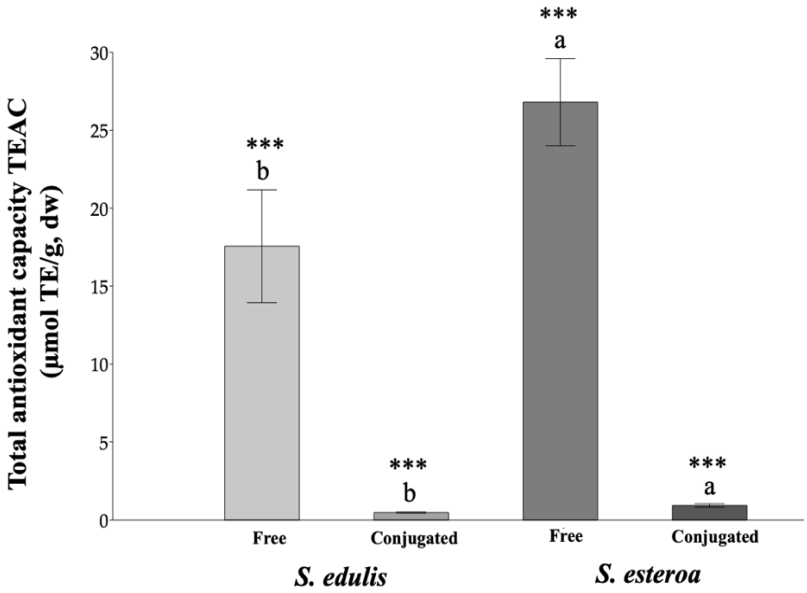

Figure 6. Total free and conjugated antioxidant capacity by TEAC (µmol ET/g, dw: dry weight) of methanolic and alkaline extracts of *S. edulis* and *S. esteroa*. Bars correspond to the mean ± standard deviation of three replicates. Superscripts a and b between bars indicate statistically significant differences between species (t-Student test, $p \leq 0.001$).

Climate and growth conditions influence the content of phenolic compounds and, in consequence, the antioxidant activity in the studied plants; previous studies reported this effect for cultivated and

wild *Mesembryanthemum nodiflorum*, *Suaeda maritima*, and *Sarcocornia fruticosa*, where the wild halophytes presented more antioxidants as an adaptive mechanism to the extreme growth conditions [75].

Likewise, the concentration, the intermolecular hydrogen bonds, and the electron-subtracting or electron-donating effect of these compounds are relevant since there are also additive, antagonistic (gallic + vanillic), and synergistic (ferulic + p-Coumaric) effects of the combination of compounds [76]. In this sense, it is remarkable that some of them could be present in the studied halophytes, with an expected antioxidant activity.

3.4. Identification of total phenols and flavonoids by UHPLC-DAD

The results suggest interesting contents in phenolic acids and flavonoids (Figure 7), whose determined values are in the following sections.

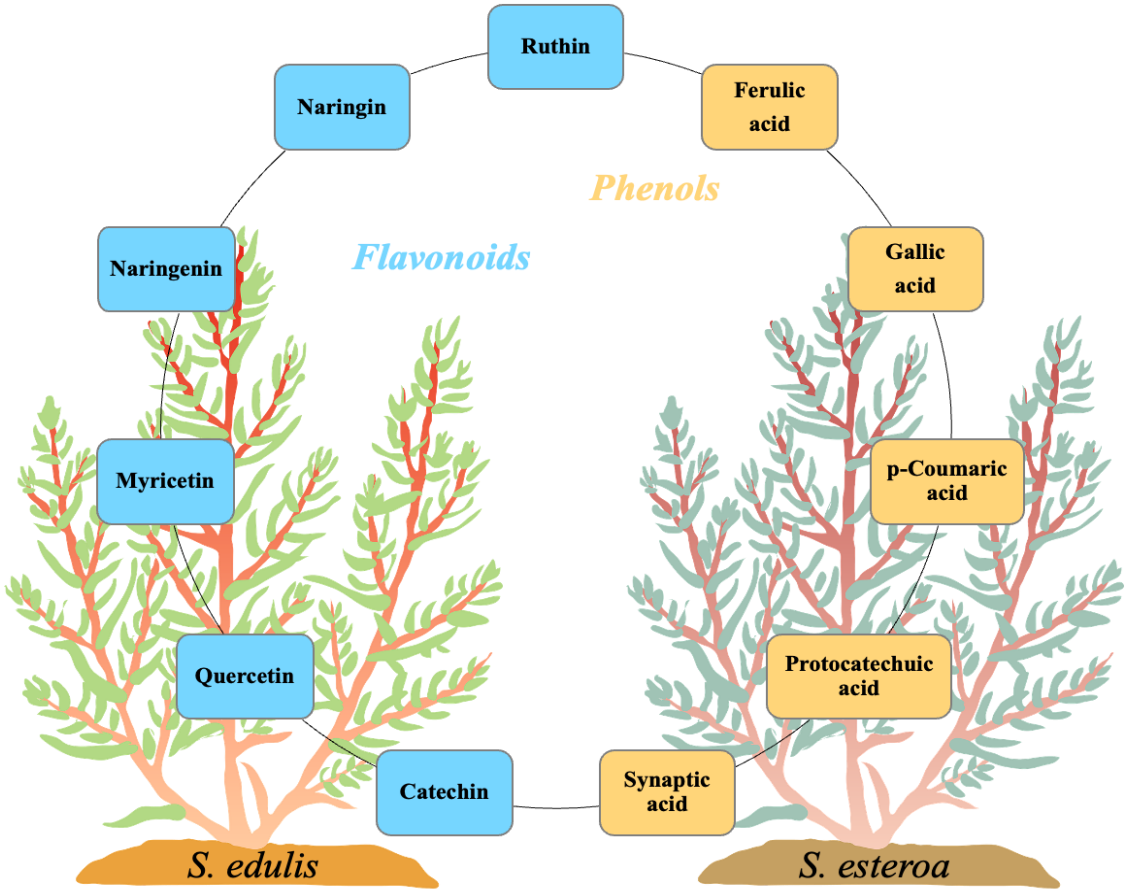

Figure 7. Flavonoids and phenolic acids identified in *S. edulis* and *S. esteroa*.

Through the related conversion of carbohydrates, precursors derived from glycolysis, and pentose phosphate pathways, the shikimate pathway is the metabolic pathway to form aromatic amino acids in plants [70]. From amino acids, glucosinolates, phytoalexins, alkaloids, auxins, tocopherols, suberin, cyanogenic glycosides, hydroxycinnamic acids, and others are synthesized [77]. From phenylalanine, phenylalanine ammonium-lyase catalyzes the deamination of phenylalanine to form trans-cinnamic acid, which then is hydroxylated at the C4 position of the aromatic ring, originating cinnamate 4-

hydroxylase, then generating p-Coumaric acid, which precedes the other hydroxycinnamic acids [78,79]. Through this pathway, chorismate (3-dehydroquinate and 3-dehydroshikimate) act as precursors, whereas, via the phenylpropanoid pathway, t-cinnamic acid deamination by CoA-dependent non-oxidative pathways, CoA-dependent β-oxidative pathways, and CoA-independent β-oxidative pathways hydroxybenzoic acids can be formed [80,81]. On the other hand, flavonoids, through phenylalanine, are transformed by enzymatic action into 4-coumaroyl-CoA, which interacts with reductase enzymes, isomerases, and hydroxylases, among others, modifying the basic structure of flavonoids and leading to the formation of the different subclasses [82]. These mechanisms promote the formation of such phenolic compounds, which are reasonably expected in the halophytes under study since they form signaling compounds, antioxidants, and others, which allow the plant to survive in saline environments [12,83,84].

We identified a set of compounds, including p-Coumaric acid, ferulic acid, synaptic acid (hydroxycinnamics), protocatechuic acid, gallic acid (hydroxybenzoic's), quercetin, myricetin, rutin (flavonols), naringenin, naringin (flavonones), and catechin (flavan-3-ols), according to the retention times and spectra of each compound, both in *S. esteroa* and *S. edulis* of both fractions (free and conjugated). Of the phenolic acids, ferulic and gallic acids were the most representative. Among these in the free fraction, ferulic acid from *S. edulis* had a significantly higher content when compared to *S. esteroa*. On the other hand, the concentration of gallic acid was much higher in *S. edulis*; however, *S. esteroa* presented high levels of synaptic acid (Table 3). Other studies reported similar results in *Arthrocnemum indicum*, where trans-ferulic acid, caffeic acid, and p-Coumaric acid, among others, were found [85]. In addition, gallic acid, chlorogenic acid, and p-Coumaric acid were found in *Inula crithmoides* and *Raphanus raphanistrum*, respectively [86].

In this sense, Hajlaoui et al. [85] explained for *A. indicum* that the highest antioxidant activity of shoot extracts towards the DPPH test may be due to its polyphenol contents; these compounds might be highly involved in the biological activity of the extract. They also found trans-ferulic acid (4-hydroxy-3-methoxycinnamic acid) (CC50 mg/mL), which is known for its potent antioxidant activity. Meanwhile, *in Sarcocornia* collected from different regions of the Iberian Peninsula, the trans-cinnamic acid showed concentrations, while the ferulic acid of some plants sampled, such as *Arthrocnemun*, was significantly observed [87].

The presence of these compounds in plants may be due to various reasons; for example, ferulic acid is an abundant compound in the cell walls of plants of the commelinids orders, while a small amount can be found in the cell walls of dicots, solanales, brassicaceae, and others [88]. In grasses, ferulic acid is linked by ester bonds to the arabinoxylan side chain, forming a structural part of the lignin and cell walls [89], while in halophytes, other reports suggest that ferulic acid has a relevant role in the salt gland's function, which helps in the secretion of salt from the plants [90]. In contrast, gallic acid is present in almost all parts of plants in its free state or as a constituent of tannins [91]. Among other functions, it regulates the induction of stress tolerance in plants, inducing the synthesis of antioxidant enzymes, phenols, flavonoids, ascorbate, and others [92]. Therefore, our results reflect the dynamism of phenolic compounds, which do not vary in concentration in some studies, such as *A. indicum*, a halophyte plant abundant in coastal marshes of Europe, Southwest Asia, and North Africa, where rutin reflects values equally high to those found in *S. edulis* [85].

Regarding flavonoids (free fraction), quercetin in *S. esteroa* and rutin in *S. edulis* presented high concentrations with significant differences (Table 3). These flavonoids in the studied halophytes help counteract ROS species excessively synthesized by the photosynthetic electron transport chain due to

environmental stresses that plants tolerate. In this sense, previous reports conclude that flavonoids perform many functions, like regulating cell growth and protecting against biotic and abiotic stresses [93].

Table 3. Identification of total free phenolic acids and flavonoids in *S. edulis* and *S. esteroa* by UHPLC-DAD. The compounds analyzed are listed in alphabetical order.

Compounds		Species	
		S. edulis	*S. esteroa*
Free total phenolic acids (μg/g, dw)	Ferulic	4467.812 ± 157.826 $^{a\,**}$	2543.170 ± 387.379 $^{b\,**}$
	Gallic	3388.038 ± 700.462 $^{a\,**}$	1.405 ± 0.110 $^{b\,**}$
	p-Coumaric	87.876 ± 7.817 $^{a\,**}$	61.707 ± 4.449 $^{b\,**}$
	Protocatechuic	191.351 ± 28.674 $^{a\,**}$	53.601 ± 0.206 $^{b\,**}$
	Synaptic	103.163 ± 3.593 $^{b\,**}$	858.769 ± 169.246 $^{a\,**}$
Free total flavonoids (μg/g, dw)	Catechin	6.408 ± 0.886 $^{b\,**}$	123.479 ± 27.704 $^{a\,**}$
	Quercetin	230.503 ± 69.148 $^{b\,**}$	1030.510 ± 248.152 $^{a\,**}$
	Myricetin	163.878 ± 27.843 $^{a\,**}$	54.720 ± 5.278 $^{b\,**}$
	Naringenin	82.574 ± 8.739 ^{ns}	99.943 ± 8.705 ^{ns}
	Naringin	44.881 ± 5.809 $^{b\,***}$	258.963 ± 20.757 $^{a\,***}$
	Rutin	15501.879 ± 822.020 $^{a\,***}$	0.437 ± 0.060 $^{b\,***}$

Notes: μg/g, dw (micrograms/g sample, dry weight); numbers correspond to the mean ± standard deviation of three replicates; superscripts ns between columns indicate statistically non-significant differences between species (t-Student test, $p > 0.05$); superscripts a and b between columns indicate statistically significant differences between species (t-Student test, $p \leq 0.01$ is indicated with **, $p \leq 0.001$ is indicated with ***).

In the case of quercetin, synthesized from the phenylpropanoid pathway, it is a molecule with a flavon structure C6 (ring A) -C3 (ring C) -C6 (ring B), of which several structural variations occur [94]. In plants, quercetin is involved in protection against ultraviolet light [95], in enhancing nutrient and water uptake [96], is an inhibitor of auxin transport [97], is involved in protein modification [98], and helps in ROS scavenging [99]. Other authors reported concentrations of 1 to 1359 mg/100 g of quercetin in tomato, onion, grape, and oregano [100], whereas, in various Brazilian halophytes, concentrations between 4 to 18 μg/g to the absence of this compound have been described [101]. Rutin, on the other hand, is a flavonol that is synthesized through the phenylpropanoid pathway by flavone synthase [102]; in plants, it functions in the same way as the rest of flavonoids, participating as a protector against ultraviolet radiation, salinity, and oxidative stress, being structurally linked to the hydrophilic part of sugar [103]. In plants such as *Chrysanthemum morifoilum*, rutin is increased by water stress [104], while in halophytes such as *Salicornia patula*, it promotes tolerance to salinity [105]. Similar results are discussed for *Tamarix africana*, *Arthrocnemum macrostachyum*, *Suaeda fruticose* [106], *M. nodiflorum*, *S. maritima*, *Suaeda fruticose* [107], *A. macrostachyum*, *Halimione portulacoides*, and *Salicornia europaea* [108]. Therefore, the presence of this compound in high concentrations responds to the growth conditions of the plants studied.

Among the phenolic compounds in plants, those found conjugated to polysaccharides, peptides, or oligosaccharides have been shown to possess anti-inflammatory properties, particularly in the colon after their hydrolysis by bacteria of the intestinal microbiota [61]. In halophytes, conjugated flavonoids participate in pigmentation and adaptation to the marine environment [109]. *S. edulis* and *S. esteroa* reflected considerable concentrations of ferulic acid and synaptic acid, contrasting with low

concentrations of flavonoids of the conjugated fraction; however, *S. esteroa* evidenced a significant concentration of naringenin (Table 4).

Table 4. Identification of total conjugated phenolic acids and flavonoids of *S. edulis* and *S. esteroa* by UHPLC-DAD. The compounds analyzed are listed in alphabetical order.

Compounds		Species	
		S. edulis	*S. esteroa*
Conjugated total phenolic acids (μg/g, dw)	Ferulic	202.997 ± 52.344 ^{ns}	220.891 ± 5.725 ^{ns}
	Gallic	51.884 ± 5.145 ^{a***}	5.235 ± 0.198 ^{b***}
	p-Coumaric	36.112 ± 8.521 ^{ns}	32.963 ± 0.305 ^{ns}
	Protocatechuic	42.972 ± 3.661 ^{a***}	16.598 ± 1.821 ^{b***}
	Synaptic	638.921 ± 85.105 ^{ns}	716.127 ± 43.578 ^{ns}
Conjugated total flavonoids (μg/g, dw)	Catechin	0.547 ± 0.055 ^{b**}	8.744 ± 1.485 ^{a**}
	Quercetin	51.546 ± 12.718 ^{ns}	50.901 ± 10.654 ^{ns}
	Myricetin	50.406 ± 0.787 ^{a***}	39.337 ± 0.697 ^{b***}
	Naringenin	54.341 ± 3.020 ^{b*}	100.497 ± 25.859 ^{a*}
	Naringin	37.415 ± 0.621 ^{a*}	26.594 ± 4.853 ^{b*}
	Rutin	0.356 ± 0.103 ^{ns}	0.386 ± 0.021 ^{ns}

Notes: μg/g, dw (micrograms/gram sample, dry weight); numbers correspond to the mean ± standard deviation of three replicates; superscript ns between columns indicate statistically non-significant differences between species (t-Student test, $p > 0.05$); superscripts a and b between columns indicate statistically significant differences between species (t-Student test, $p \leq 0.05$ is indicated with *, $p \leq 0.01$ is indicated with **, $p \leq 0.001$ is indicated with ***).

The identification of naringenin in halophytes may be due to its participation in ultraviolet protection, defense against pathogens, attraction of pollinators, and even regulation of plant growth [110]. Other authors described the function of naringenin in different halophytes, such as *Rhizophora racemose* [111] and *Suaeda japonica* [112]. In plants, the phenolic compounds are present in protective central vacuoles, subdermal cells of leaves, and epidermal cells; some of these compounds are bound to cell walls, waxes, and on the external surfaces of plants [113]. These compounds help in the transduction of light energy [114], are part of phytohormones related to circadian rhythms [115], help by exerting allelochemical effects that influence the inorganic and organic nutrients surrounding the plants [116], and even form complexes with proteins helping leaf judgment [117]. Under biotic stress conditions, phenolic compounds participate as physical barriers against herbivores, are part of the resistance to microorganisms, and even lead to the inactivation of insect digestive proteins, causing their death [113]. On the other hand, due to abiotic stress conditions (salinity, UV, drought, pesticides, and high temperatures), phenolic compounds act as antioxidants [118–120].

Therefore, under different growth and development conditions, *S. edulis* and *S. esteroa* formed the necessary compounds to survive, some of which we identified. However, although *S. esteroa* presented a higher content of free total phenols and antioxidant activity, possibly other compounds that favored the increase of these activities could not be identified by the mentioned techniques. An example of this is the identification of different phenolic compounds in other halophytes, such as 3,4-dihydroxybenzoic acid, vanillic acid, rosmaric acid, cinnamic acid [75], 5-O-feruloylquinic acid, neochlorogenic acid [111], and trans-ferulic acid among others [121].

Phenolic compounds provide several benefits, from antioxidant, anticancer, antimicrobial, and

anti-inflammatory to neuroprotective and antidiabetic properties [12]. Accordingly, the search for diverse and more effective sources of phenolic compounds is ongoing. The need to expand the diversity of these compounds highlights this interest, as well as sustainable and locally available sources [28,122]. In this scenario, a novel investigation of various phenolic compounds in some halophytes reveals unique characteristics, such as their resistance to climate change, tolerance to salinity, and ability to thrive in extreme conditions. These properties position the species *S. edulis* and *S. esteroa* as sustainable agricultural options that could be considered new sources of phenolic compounds for the development of foods or nutraceuticals that ultimately help to counteract chronic diseases related to excess weight and obesity, as already used in different halophytes traditionally consumed due to their organoleptic and medicinal properties [123], such as those of the genus *Salicornia* (Chenopodiaceae), which is appreciated and valued as gourmet food for its salty flavor [124].

Flavonoids and phenolic acids make up one of the most pervasive groups of plant phenolics; their importance in plants and human health motivates the generation of knowledge to have a deeper understanding of flavonoids, their biological activities, and their potential as therapeutic agents. The effect of dietary phenolics is currently of great interest due to their antioxidative and possible anticarcinogenic activities [125]. Phenolic compounds are reactive metabolites in a wide range of plant-derived foods; they work as terminators of free radicals and chelators of metal ions capable of catalyzing lipid oxidation [126]. According to the above, both *Suaeda* species are promissory to enrich the basic basket with inherent benefits to human health.

For example, *S. edulis* reflected relatively high values of free ferulic acid (4467.812 μg/g) and gallic acid (3388.038 μg/g); on the other hand, *S. esteroa* reflected the highest values for ferulic acid (2543.170 μg/g) and synaptic acid (858.769 μg/g). For *S. edulis*, the free flavonoids with the highest values were rutin (15501.879 μg/g) and quercetin (230.503 μg/g), while for *S. esteroa* they were quercetin (1030.510 μg/g) and naringin (258.963 μg/g) (Table 3).

4. Conclusions

S. esteroa reflected the highest content of total phenols (free and conjugated) and antioxidant activity. In both *Suaeda* species, ferulic acid and gallic acid of the free fraction had the highest concentration compared to the other phenolic acids. When comparing ferulic acid and gallic acid among the halophytes, *S. edulis* presented significantly higher concentrations. Quercetin for *S. esteroa* and rutin for *S. edulis* were the most representative flavonoids of the free fraction for each species. On the other hand, regarding the conjugated fraction, ferulic and synaptic acids presented the highest concentration in the halophytes studied, but did not evidence significant differences. We found low flavonoid concentrations of the conjugated fraction but observed a considerable concentration of naringenin in *S. esteroa*. The halophytes *S. edulis* and *S. esteroa* are emerging plant resources, potentially new options for developing novel functional foods due to valuable concentrations of phenolic compounds in their matrix. The utilization of these plants could also help to counteract some chronic degenerative diseases related to obesity, and they can help to improve saline soils and marginal lands and solve food shortages in some regions with water scarcity and high temperatures.

Use of AI tools declaration

The authors declare they did not apply any Artificial Intelligence (AI) tool in the creation of this article.

Acknowledgments

Part of this research was funded by the National Council for the Humanities, Sciences and Technologies of Mexico (CONAHCyT) through the grant supported with the scholarship number 766309 for the first author's doctoral studies, which facilitated her stay in Hermosillo, Sonora, Mexico. This project was supported by the Center for Biological Research of Northwest México S.C. (CIBNOR) (Project 10025-PAZA), with the collaboration of the University of Sonora (UNISON). The first author would like to thank the engineer, and producer of romeritos in the Chinampa area Prospero Rosales for his support for the field trip to his *S. edulis* production site. To the technician Pedro Luna García of the Experimental Station of CIBNOR, for his support in the local field trip to the site of establishment, and collection of *S. esteroa* at Balandra beach, La Paz, B.C.S., Mexico. To Dr. Miguel Angel Zavala Sánchez, M. en C. Raúl Calleros Flores of the Autonomous Metropolitan University (UAM-Xochimilco) in the Department of Biological Systems. To Dr. Claudia Judith Hernández Guerrero of the Interdisciplinary Center for Marine Sciences (CICIMAR-IPN) in the Microbiology, and Molecular Biology Laboratory for their support, and assistance in the processing, and drying of the samples of *S. edulis*, and *S. esteroa*. And to Dr. Norma Julieta Salazar López from the School of Medicine Mexicali of the Autonomous University of Baja California (UABC) for supporting me in the training with the UHPLC-DAD equipment.

Conflict of interest

The authors declare no conflicts of interest. The funders had no role in the design of the study; in the collection, analyses, or interpretation of data; in the writing of the manuscript, or in deciding to publish it.

Author contributions

FRCB and ETD: Conceptualization; FRCB, ETD, AARH and RMRS: Data curation; FRCB, ETD, AARH, FAN, LABS and RMRS: Formal analysis; ETD and RMRS: Funding acquisition; FRCB and ETD: Investigation; FRCB, ETD, AARH and RMRS: Methodology; ETD: Project administration; ETD and RMRS: Resources; FRCB, ETD, AMN and ROMR: Software; AARH and RMRS: Supervision; FRCB and RMRS: Validation; FRCB, AARH and RMRS: Visualization; FRCB, AARH and ETD: Writing—original draft; FRCB and ETD: Writing—review and editing. All authors have read and agreed to the published version of the manuscript.

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