Science of the Total Environment 869 (2023) 161806

Contents lists available at ScienceDirect

Science of the Total Environment

journal homepage: www.elsevier.com/locate/scitotenv

Soil physicochemical properties associated with the yield and phytochemical composition of the edible halophyte *Crithmum maritimum*

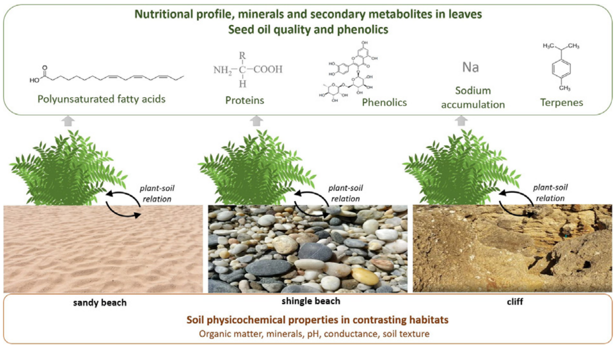
Raquel Martins-Noguerol [a,b,*], Luis Matías [a], Ignacio M. Pérez-Ramos [b], Xoaquín Moreira [c], Marta Francisco [c], Justo Pedroche [d], Cristina DeAndrés-Gil [d], Eduardo Gutiérrez [b], Joaquín J. Salas [d], Antonio J. Moreno-Pérez [d], Anthony J. Davy [e], Sara Muñoz-Vallés [f], Manuel Enrique Figueroa [a], Jesús Cambrollé [a]

[a] *Departamento de Biología Vegetal y Ecología, Facultad de Biología, Universidad de Sevilla, Profesor García González s/n, E-41012 Sevilla, Spain*
[b] *Instituto de Recursos Naturales y Agrobiología de Sevilla (IRNAS-CSIC), P.O. Box 1052, 41080 Sevilla, Andalucía, Spain*
[c] *Misión Biológica de Galicia (MBG-CSIC), Apdo. 28, 36080 Pontevedra, Galicia, Spain*
[d] *Instituto de la Grasa (IG-CSIC), Building 46, UPO Campus, Ctra. de Utrera km 1, 41013 Sevilla, Spain*
[e] *Centre for Ecology, Evolution and Conservation, School of Biological Sciences, University of East Anglia, Norwich NR4 7TJ, United Kingdom*
[f] *Departamento de Agronomía, Escuela Técnica Superior de Ingeniería Agronómica, Universidad de Sevilla, Seville 41013, Spain*

HIGHLIGHTS

- Sea fennel performs well in diverse dry coastal habitats, mainly beaches and cliffs.
- It yields a wide spectrum of useful phytochemicals and secondary metabolites.
- Lower substrate fertility enhanced its protein and phenolic content.
- Soil texture and microelement content modified the nutritional quality of seed oil.
- Sea fennel has potential as an alternative crop in saline, nutrient-poor settings.

GRAPHICAL ABSTRACT



ARTICLE INFO

Editor: Charlotte Poschenrieder

Keywords:
Halophyte
Sea fennel
Plant-soil relation
Plant valorization
Nutrient composition
Phenolics

ABSTRACT

There is growing interest in the consumption of halophytes due to their excellent nutritional profile and antioxidant properties, and their cultivation offers viable alternatives in the face of irreversible global salinization of soils. Nevertheless, abiotic factors strongly influence their phytochemical composition, and little is known about how growing conditions can produce plants with the best nutritional and functional properties. *Crithmum maritimum* is an edible halophyte with antioxidant properties and considerable potential for sustainable agriculture in marginal environments. However, it is found naturally in contrasting habitats with variable soil physicochemical properties and the extent to which edaphic factors can influence plant performance, accumulation of phytochemicals and their quality remains unknown. We investigated the influence of soil physicochemical properties (texture, pH, electrical conductivity, organic matter content and mineral element concentrations) on growth and reproductive performance, nutritional traits, and the accumulation of specific metabolites in *C. maritimum*. Soil, leaf and seed samples were taken from eight *C. maritimum* populations located on the southern coasts of Spain and Portugal. We found greater vegetative growth and seed production in coarser, sandier soils with lower microelement concentrations. The nutritional traits of leaves varied, with soil organic matter and macronutrient content associated with reduced leaf Na, protein and phenolic (mainly flavonoid) concentrations, whereas soils with lower pH and Fe concentrations, and higher clay content yielded plants with lower leaf Zn concentration and greater accumulation of hydroxycinnamic acids. The nutritional value of

---

* Corresponding author at: Departamento de Biología Vegetal y Ecología, Facultad de Biología, Universidad de Sevilla, Profesor García González s/n, E-41012 Sevilla, Spain.
E-mail address: rmartins18@us.es (R. Martins-Noguerol).

http://dx.doi.org/10.1016/j.scitotenv.2023.161806
Received 15 September 2022; Received in revised form 19 January 2023; Accepted 20 January 2023

the seed oil composition appeared to be enhanced in soils with coarser texture and lower microelement concentrations. The accumulation of specific phenolic compounds in the seed was influenced by a wide range of soil properties including texture, pH and some microelements. These findings will inform the commercial cultivation of *C. maritimum,* particularly in the economic exploitation of poorly utilized, saline soils.

1. Introduction

Halophytes are salt-tolerant plants commonly found in coastal areas worldwide, where they grow under severe environmental constraints from salinity, wind exposure, and drought (Lokhande and Suprasanna, 2012). Due to their tolerance of high salinity, low nutrient availability and other abiotic stresses, halophytes offer a promising approach for sustainable agriculture in marginal environments (Agudelo et al., 2021). Leaves of halophytes have been traditionally consumed by local populations and are commonly used for animal feed, phyto-fuels and fertilizers, as well as in phytoremediation and desalination processes (Shaer and Attia-Ismail, 2015). It is now recognised that halophytes represent an excellent source of biomolecules with important nutritional and health benefits (e.g. Agudelo et al., 2021). Consequently, there is growing interest in the study of wild halophytes to promote their use as crops and for different industrial applications. Importantly, they could offer opportunities for production in the light of shrinking arable land areas, as the irreversible global salinization of soils and fresh waters becomes a serious constraint to worldwide crop productivity.

Despite the potential of halophytes as crops, especially in environments with harsh climates and poor soil conditions, the factors that could affect their leaf phytochemicals remain poorly understood. Some well-known factors regulating leaf phytochemicals are physical or abiotic, including soil nutrients, water or light availability, and mechanical stress (Gil et al., 2014; Lopes et al., 2021). In particular, soil nutrient availability, salinity, and permeability can influence plant phytochemistry by modulating the costs associated with their production and deployment of phytochemicals, through physiological constraints on metabolism (Zobayed et al., 2007; Griesser et al., 2015). In addition, these factors might affect other plant functions such as growth and reproduction, which involve trade-offs with plant biochemistry (Akula and Ravishankar, 2011). However, studies distinguishing direct and indirect interactions between soil conditions, halophyte growth and reproduction, and leaf phytochemicals have been scarce.

Crithmum maritimum L. (Apiaceae), known as sea fennel or rock samphire, is a facultative halophyte widely distributed in coastal habitats throughout Western Europe that is well-known for a variety of food and other uses (Renna, 2018). Its leaves display high antioxidant and nutritional value (Nabet et al., 2017; Sánchez-Faure et al., 2020), and its seeds contain appreciable amounts of good-quality, edible oil and secondary metabolites with different potential industrial applications (Pavela et al., 2017; Martins-Noguerol et al., 2022a; Sousa et al., 2022). Apart from its nutritional value, *C. maritimum* could be a viable alternative crop in nutrient-poor or degraded soils that are not suitable for conventional species (Karkanis et al., 2022). However, considerable variation in chemical features can be found depending on its geographic origin (Cunsolo et al., 1993; Özcan et al., 2006; Meot-Duros and Magné, 2009; Sánchez-Faure et al., 2020) and the accumulation of secondary metabolites can vary depending on the growing conditions and the intensity of abiotic stresses (Martins-Noguerol et al., 2022b; Castillo et al., 2022). Nevertheless, few studies have investigated yield and phytochemical composition in relation to the great variation in physicochemical soil properties evident in its contrasting habitats, including cliffs, shingle beaches and sandy beaches (Meot-Duros and Magné, 2009; Martins-Noguerol et al., 2022a).The present work aimed to (i) identify the physicochemical soil properties that promote *C. maritimum* yield and performance in contrasting natural habitats and (ii) evaluate the relative importance of the edaphic factors that affect the nutritional status and accumulation of phytochemicals in *C. maritimum* leaves and seeds. To further these objectives, soil, leaf and seed samples were taken from eight *C. maritimum* populations located on the southern coasts of Spain and Portugal, reflecting the wide range of ecosystems where the species naturally grows. We examined soil characteristics (texture, pH, electrical conductivity, organic matter content and mineral element concentrations) with the overarching aim of evaluating their relative influence on the chemical composition of leaves and seeds (including proteins, lipids, minerals, phenolics and terpenes). This constitutes the first comprehensive analysis of edaphic factors affecting the nutritional and antioxidant profiles in a halophyte. It seeks to inform and re-evaluate the use of this wild halophyte as a potential crop in sustainable cropping systems, particularly on poor or degraded soils.

2. Materials and methods

2.1. Field sampling and plant material

Eight wild populations of *C. maritimum* were selected for sampling along the southern coast of Spain and Portugal in September 2019. Individual populations were 13–785 km apart and comprised at least 30 adult plants each. These populations encompassed different habitat topographies and soil properties (Fig. 1), representing the main habitat types which it naturally inhabits: sandy beaches, shingle beaches and cliffs (Atia et al., 2011). At each site, we selected 12 typical adult plants of similar height (average plant height of 44.59 ± 1.62 cm [mean ± SE]) and separated by at least 2 m. For each plant, we recorded the distance to the tide line and collected between 20 and 25 randomly selected and fully developed leaves for chemical analyses of proteins, phenolics and mineral nutrients. Samples were kept under refrigeration, transported to the lab and stored at −20 °C. For terpene analyses, leaves were placed in dry ice and then kept at −80 °C. For lipid analyses, leaf samples were kept in 2-propanol, transported to the lab and then stored at −20 °C. We also collected mature fruits from each plant for analyses of seed lipid and phenolic composition.

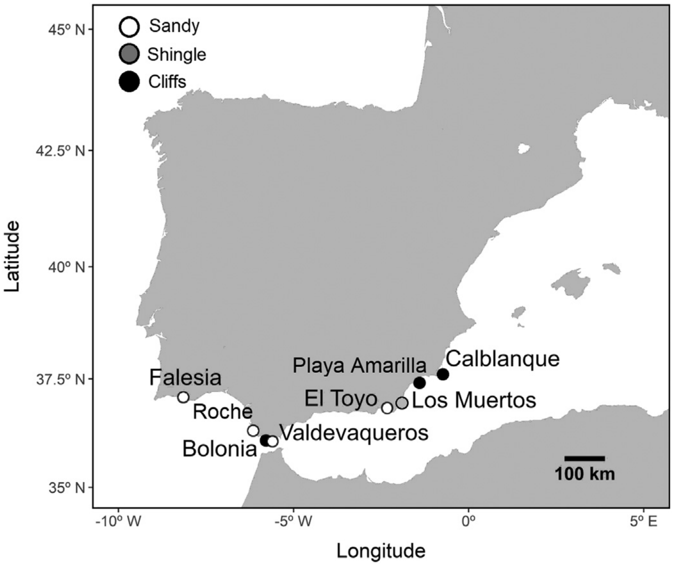


Fig. 1. Location of the study populations of *Crithmum maritimum.* Map showing the location and habitat-type of the eight populations of *C. maritimum* sampled along the coasts of southern Portugal and Spain.

2.2. Measurements of physicochemical soil variables

Topsoil samples (0–30 cm depth) were collected at a distance of 10–20 cm from the limit of the projected plant canopy of each plant sampled. Measurements of electrical conductivity, pH, organic matter content and soil texture were made in the laboratory. Conductivity was determined in a 1:5 (*w/v*) soil:water suspension using a conductivity meter (Crison-522, Spain). pH was determined potentiometrically in a soil:water (1:2.5) suspension with a digital meter (Crison pH -25, Spain). Organic matter content was estimated by muffle furnace calcination (Muffle HD-230, Hobersal S.L., Spain) at 450 °C for 4 h. For soil texture analysis, we removed the coarse elements (> 2 mm soil fraction) by sieving to estimate the percentage of gravel. Coarse and fine sand proportions were determined by sieving in the 2–0.5 mm soil fraction. Fine sand, silt and clay percentages were determined in the <0.5 mm fraction according to the Bouyoucos hydrometer method (Bouyoucos, 1962). We quantified the concentrations of soil macronutrients (Ca, K, Mg, N, P, S) and microelements (Al, As, B, Ba, Cr, Cu, Fe, Li, Mn, Na, Ni, Pb, Sr, V, Zn) in the upper 30 cm of the soil. Previously, samples were oven-dried at 40 °C for 48 h, homogenized by sieving to <2 mm in order to remove large stones and dead plant material, and ground to <1 mm. Then, samples were digested with HNO_3 and HCl and analysed by inductively coupled plasma optical emission spectroscopy (ICP-OES) with a Varian ICP 720-ES (Agilent Technologies, Inc., USA). Total nitrogen concentration was estimated by the N- Kjeldahl method (Kjeldahl, 1883).

2.3. Plant performance measurements

We measured different traits related to plant performance, including vegetative height and volume, and seed production. Plant volume was calculated from measurements of maximum and minimum diameter and maximum height, assuming a semi-spheroid form. To estimate seed yield, the total number of umbels per plant was recorded and then seven randomly-selected umbels per plant were collected to count the total number of fruits per umbel (each fruit contains a single seed). The fruits were weighed and then the seeds were removed and weighed separately, using a precision balance.

2.4. Mineral elements in leaves

Total foliar concentrations of mineral elements were analysed in 0.5 g oven-dried samples by inductively coupled plasma optical emission spectroscopy (ICP-OES Varian ICP 720-ES), as described in Martins-Noguerol et al. (2022b). The total foliar nitrogen (N) content (expressed in %) was estimated by the Kjeldahl method (Kjeldahl, 1883).

2.5. Lipid and fatty acid composition in leaves and seeds

We extracted total lipid content from approximately 1 g of leaf tissue or 20 mg of seeds according to Hara and Radin (1978). Methylation of fatty acids was performed by adding 3 mL of a mixture containing methanol/toluene/sulphuric acid (88:10:2, *v*/v/v) and then the mixture was heated at 80 °C for 1 h (Garcés and Mancha, 1993). Fatty acid methyl esters (FAMEs) were extracted with heptane and analysed by GLC using a Perkin-Elmer Clarus500 gas chromatograph and a Supelco SP-2380 capillary column (Supelco, USA). For quantification of fatty acids, heptadecanoic acid (17:0, Sigma-Aldrich, USA) was used as internal standard. The identification of different methyl esters was performed by comparison with a combination of standards. The nutritional value of fatty acid composition was assessed by calculating the polyunsaturated to saturated fatty acid ratio (PUFA/SFA) and the atherogenicity index (AI) and thrombogenicity index (TI) according to Ulbricht and Southgate (1991), which are commonly used to evaluate the fatty acid composition in relation to human cardiovascular health (Chen and Liu, 2020).

2.6. Protein content in leaves

Total protein content was estimated by multiplying Kjeldahl total nitrogen content of leaves by a factor of 4.43 according to Yeoh and Wee (1994) for angiosperms.

2.7. Identification and quantification of phenolic compounds in leaves and seeds

Phenolic compounds were extracted from 20 mg of dried material (leaves or seeds) with 0.25 mL of 70 % methanol in an ultrasonic bath for 15 min, followed by centrifugation. The supernatant was filtered through a 0.20-μm micropore PTFE membrane and placed in vials for chromatographic analysis (Moreira et al., 2021). For chemical identification of the polyphenol composition we used ultra-performance liquid chromatography coupled with an electrospray ionization quadrupole (Thermo Dionex Ultimate 3000 LC) time-of-flight mass spectrometry (UPLC-Q-TOF-MS/MS) (Compact™) (Bruker Daltonics GmbH, Germany). Chromatographic separation was performed in a Kinetex™ 2.6 μm C18 82–102 Å, LC Column 100 × 4.6 mm column using a binary gradient solvent mode consisting of 0.05 % formic acid in water (solvent A) and acetonitrile (solvent B). The following gradient was used: from 10 % to 30 % B (0–5 min), from 30 to 50 % B (5–10 min), from 50 to 100 % B (10–12 min), hold 100 % B until 14 min, from 100 % to 10 % B (14–15 min), hold 10 % B until 17 min. The injection volume was 3 μL. The flow rate was established at 0.4 mL min^{-1} and column temperature was controlled at 35 °C. MS analysis was operated in a spectra acquisition range from 50 to 1200 *m/z*. Negative (−) ESI modes were used under the following specific conditions: gas flow 8 L/min, nebulizer pressure 38 psi, dry gas 7 L/min, and dry temperature 220 °C. Capillary and end plate offset were set to 4500 and 500 V, respectively. MS/MS analysis was performed based on the previously determined accurate mass and RT, and fragmented by using different collision energy ramps to cover a range from 15 to 50 eV. Individual compounds were identified based on the data obtained from the standard substances or published literature including RT, λ_{max}, ($[M–H]^-$), and major fragment ions.

For the quantitative analysis of phenolic compounds, 10 μL of each sample was then analysed using the column and conditions described previously, in an UHPLC (Nexera LC-30 AD; Shimadzu) with a Nexera SIL-30 AC injector and one SPD-M20A UV/VIS photodiode array detector (Shimadzu, Japan); see Moreira et al. (2021) for more details of the chromatographic analyses. Recording of chromatograms was performed at 330 nm. The flavonoids were quantified as rutin equivalents and hydroxycinnamic acids as chlorogenic acid equivalents. We quantified these phenolic compounds by external calibration using calibration curves at 0.25, 0.5, 1, 2 and 5 μg/ mL.

2.8. Identification and quantification of terpenes in leaves

Terpenes were extracted from 300 mg of ground fresh material with 1 mL of 70 % methanol in an ultrasonic bath for 20 min and samples stored at 4 °C for 24 h. We also added dodecane (Merck, #1.09658.0005) as the internal standard solution (100 ppm of dodecane in *n*-hexane). We injected the samples (1 μL) into a gas chromatograph (GC, Thermo Finnegan Trace GC Ultra, Waltham, MA, USA) with a mass spectrometer (MS) detector that was fitted with a 30 m × 0.25 mm × 0.25 μ film thickness ZB-5MSi (Phenomenex, UK) in single ion monitoring mode (SIM: *m/z* 68, 69, 77, 79, 92, 93, 94, 105, 119, 121, 136, 148, 161, 175) used to visualise known terpene fragments. The GC was operated in split mode (50 mL min^{-1}) with helium as the carrier gas (flow rate 1 mL min^{-1}). The GC oven temperature program was: 2 min hold at 60 °C, 10 °C min^{-1} ramp to 70 °C, 15 min hold at 70 °C, 5 °C min^{-1} ramp to 130 °C, 30 °C min^{-1} ramp to 250 °C, and 1 min hold at 250 °C. We identified terpenes by comparing their Kováts indices, calculated relative to the retention times of a series of n-alkanes (C_8-C_{20}, Sigma-Aldrich, Merck KGaA, Darmstadt, Germany) analysed under the same chromatographic conditions, with those reported in the literature (Tsoukatou et al., 2001; Nabet et al., 2017). For each plant, we estimated the quantity of terpenes by using normalized peak areas per dry weight. The normalized peak area per dry weight of each compound was obtained by dividing their integrated peak area by the integrated peak area of the internal standard and then dividing this value by the leaf dry weight.

2.9. Statistical analyses

We summarised the variation in all soil variables (physiochemical properties and mineral elements) with a principal component analysis (PCA). Then we used Generalized Linear Mixed Models (GLMMs) to evaluate soil property effects on the characteristics of *C. maritimum* related with plant performance (plant volume, vegetative height, number of infructescences, number of seeds per infructescence, total number of seeds per plant, and fruit and seed weight), and on the phytochemistry of leaves (proteins, lipids, mineral, terpene and phenolic content) and seeds (oil and phenolic content). For this, we included the first three axes of variation in the PCA analysis and the distance to the high tide line as fixed factors, and population as a random factor. All variables were tested for normality and transformed as necessary to meet analysis assumptions. All statistical analyses were conducted with R software version 4.1.1 (R Core Team, 2021). GLMMs were performed using package "lme4" (Bates et al., 2015) and compared with the MUMIN package (Barton, 2009).

3. Results

3.1. Soil physicochemical properties

The study sites exhibited great heterogeneity in their soil physical and chemical properties (Table 1). At all of the sites soil texture was dominated by coarse sand (83.8–94.8 %) and pH was strongly alkaline (8.98–9.81). Electrical conductivity displayed values between 160.0 and 525.4 μS/cm, indicating high and variable salinity levels in these areas. Different concentrations of organic matter were found depending on site, and the concentrations and relative abundance of mineral elements were also highly variable, although all of the soils were characterised by low N and P contents (Table 1). An ordination of the soil physicochemical properties based on the first two PCA axes is shown in Table 2. The first PCA axis (hereafter "PC1 soil") explained 36.26 % of the total variation, and was clearly associated with soil texture and microelements. The microelement content as well as the percentages of fine sand and silt were negatively loaded on the axis, whereas the percentage of coarse sand was positively loaded. The second PCA axis (hereafter "PC2 soil") explained 21.70 % of the total variation and was related to organic matter content and macronutrients. Both organic matter and macronutrient contents were positively associated with this axis. The third PCA axis (hereafter "PC3 soil"), which explained 10.97 % of the total variation, was positively associated with the percentage of clay and negatively related to pH and Fe content.

3.2. Relationships between soil physicochemical properties and plant performance

The GLMMs indicated a significant positive association between most of the traits related to plant performance (plant volume, number of infructescences, number of seeds per infructescence and number of seeds per plant) and soil PC1 (Table 3). These findings indicate that plants growing in soils with higher coarse sand percentage and lower content of microelements were larger (i.e. had greater volume) and produced more seeds (Fig. 2). On the other hand, plant vegetative height was negatively correlated with soil PC2 (Table 3; Fig. 2), indicating that taller plants were growing in less fertile soils (i.e. with lower organic matter and macronutrient content). There was no detectable association between fruit or seed weight with any of the PCA axes. Both leaf N and P content, which ranged from 0.7 to 2.2 % and from 0.1 to 0.3 % (dry weight, DW), respectively, were negatively associated with soil PC2 (Table 4), indicating that the concentrations of both elements were higher in plants growing in less fertile soils.

3.3. Relationships between soil physicochemical properties and leaf metabolites

The total protein content of *C. maritimum* leaves ranged between 2.9 and 9.6 % (DW) and was negatively correlated with soil PC2 (Table 4). For mineral composition, we also found a significant negative association between the leaf content of Na, which ranged between 0.4 and 7.4 % (DW), with soil PC2, whereas Zn concentration, which ranged between 4.7 and 59.0 mg/kg DW, was negatively correlated with soil PC3 (Table 4). The total phenolic content (TPC) ranged between 18.4 and 85.0 mg/g DW and was also negatively correlated with soil PC2 (Table 4). Within TPC, we detected phenolics from two main groups in *C. maritimum* leaves: flavonoids and hydroxycinnamic acids. Whereas flavonoid content was negatively associated with soil PC2, a significant positive correlation was found between hydroxycinnamic acids and soil PC3 (Table 4). All these results indicate that plants growing in less fertile soils possessed leaves with more protein and Na and higher concentrations of phenolic compounds, including flavonoids. On the other hand, in less basic soils with more clay and lower Fe content, plants showed higher levels of hydroxycinnamic acids and lower Zn concentrations. In relation to terpenes, only monoterpenes were found in *C. maritimum* leaves and there was no detectable association between the total content of these metabolites and any of the PCA axes. The monoterpenes mainly represented in *C. maritimum* leaves (Supplementary Table 1) were analysed in the GLMM; a significant positive association was observed between p-cymene content and PC1, whereas thymol methyl ether concentration was negatively associated with PC2 (Table 4). We found no significant associations between the lipid content or fatty acid composition of leaves and any of the PCA axes.

3.4. Relationships between soil physicochemical properties and seed chemical compounds

C. maritimum seeds showed an oil content that ranged between 4.0 and 18.2 %. The oil composition had a high proportion of unsaturated fatty acids, with oleic acid (18:1) as the main monounsaturated fatty acid (MUFA) ranging between 59.3 and 79.6 % of total fatty acids, and linoleic acid (18:2) as the only polyunsaturated fatty acid (PUFA), ranging from 9.0 to 17.5 %. Palmitic acid was the most abundant saturated fatty acid (SFA), which ranged between 4.7 and 19.6 % of total fatty acids. The nutritional value of *C. maritimum* seed oil was assessed by calculating AI and TI indexes and PUFA/SFA ratio (see below). AI ranged from 0.1 to 0.7 and from 0.2 to 0.6. GLMM indicated a significant negative association between both indexes and soil PC1 (Table 5). Otherwise, the PUFA/SFA ratio (range 0.01–2.21) was positively correlated with the same axis (Table 5). These findings indicate that plants growing in soils with coarser texture and lower microelement content displayed lower AI and TI indexes together with higher PUFA percentage and PUFA/SFA ratio. These indexes are widely used to evaluate the fatty acid composition in relation to cardiovascular health. PUFA/SFA is a basic index considering just polyunsaturated and saturated fatty acids, whereas AI and TI consider the contribution of different molecular species of saturated fatty acids. Therefore, AI and TI denote the relationships between the main saturated fatty acid (C12:0, C14:0 and C16:0), which are considered pro-atherogenic and pro-thrombogenic (i.e. they favour the adhesion of lipids to cells in circulatory system to form blood clots) and unsaturated fatty acids considered anti-atherogenic and anti-thrombogenic (Chen and Liu, 2020). In relation to oil seed content, we found no significant associations between lipid content and any of the PCA axes.

Likewise, TPC of the seed was not correlated with soil PCAs but significant associations were detected for some specific phenolic compounds (Table 5). Thus, the concentrations of 3-caffeoylquinic acid, 5-caffeoylquinic acid, 3,5-dicaffeoylquinic acid and 4,5-dicaffeoylquinic acid were negatively correlated with soil PC3, indicating that they were elevated in plants growing in soils with lower clay content, and higher pH and Fe concentration. On the other hand, the concentrations of feruloyl quinic acid and quercetin-7-xyloside were negatively associated with both

Table 1

Main characteristics of the *C. maritimum* populations sampled and summary descriptive statistics of their soil physicochemical properties. Data represent means and standard errors of seven-twelve independent replicates.

Physicochemical properties		Populations							
	Units	Roche	Bolonia	Valdevaqueros	El Toyo	Los Muertos	Playa Amarilla	Calblanque	Falesia
Coordinates	–	36.314138, −6.153952	36.087543, −5.785027	36.067365, −5.695350	36.835718, −2.325802	36.956220, −1.899545	37.411292, −1.54792	37.602117, −0.731187	37,080372, −8,148,073
Habitat topography	–	sandy	cliffs	sandy	sandy with coarse elements	shingle beach	cliffs	cliffs	sandy
Average distance to the tide line	m	47.40 ± 2.78	11.64 ± 1.73	25.47 ± 2.59	20.55 ± 3.23	44.46 ± 3.47	11.67 ± 2.10	16.63 ± 2.18	28.46 ± 0.88
Organic matter	mg C/g DW	39.71 ± 13.63	26.84 ± 10.43	19.15 ± 9.15	23.78 ± 4.40	31.37 ± 9.79	101.86 ± 20.33	74.09 ± 20.48	17.41 ± 9.39
pH	–	9.42 ± 0.09	9.35 ± 0.13	9.27 ± 0.05	9.50 ± 0.11	9.81 ± 0.10	9.33 ± 0.16	9.53 ± 0.14	8.98 ± 0.22
Electrical conductivity	μS/cm	168.84 ± 33.73	175.86 ± 54.48	190.72 ± 46.35	525.54 ± 157.69	466.40 ± 88.31	409.31 ± 128.69	160.03 ± 22.67	386.58 ± 22.88
Coarse sand	%	94.80 ± 0.84	94.30 ± 0.60	92.98 ± 0.37	83.84 ± 5.94	88.78 ± 2.78	87.68 ± 2.13	93.08 ± 1.09	90.76 ± 1.06
Fine sand	%	1.05 ± 0.27	0.87 ± 0.07	2.12 ± 0.27	4.71 ± 1.36	2.98 ± 1.14	5.90 ± 1.27	2.12 ± 0.63	2.07 ± 0.28
Silt	%	2.84 ± 0.44	2.00 ± 0.49	0.86 ± 0.25	7.72 ± 2.90	6.81 ± 1.47	5.14 ± 1.02	3.38 ± 0.50	3.73 ± 0.47
Clay	%	1.28 ± 0.27	2.76 ± 0.14	4.04 ± 0.30	3.73 ± 1.88	1.41 ± 0.37	1.28 ± 0.27	1.42 ± 0.37	3.42 ± 0.64
Gravel	%	0.26 ± 0.15	0.10 ± 0.07	0.00 ± 0.00	13.50 ± 4.23	75.88 ± 7.11	8.87 ± 4.31	2.58 ± 1.18	17.58 ± 2.74
Al	mg/kg DW	1486.68 ± 535.13	1153.76 ± 249.55	1253.26 ± 662.03	4993.78 ± 661.22	24,455.17 ± 4428.43	2358.48 ± 242.11	1897.79 ± 149.68	5996.63 ± 1488.83
As	mg/kg DW	6.49 ± 0.43	3.07 ± 0.42	3.16 ± 1.25	14.53 ± 1.25	3.00 ± 0.39	66.32 ± 5.77	31.14 ± 1.27	2.55 ± 0.23
B	mg/kg DW	3.02 ± 0.20	2.62 ± 0.30	3.17 ± 0.93	2.71 ± 1.36	2.34 ± 1.00	10.16 ± 0.78	5.53 ± 0.41	2.70 ± 0.55
Ba	mg/kg DW	5.81 ± 0.82	5.69 ± 0.71	9.08 ± 3.82	28.30 ± 5.44	28.69 ± 3.76	28.26 ± 3.89	12.12 ± 0.71	45.00 ± 8.47
Ca	mg/kg DW	64,449.5 ± 3833.83	51,401.66 ± 2112.94	56,800.98 ± 2828.23	34,372.55 ± 5723.65	40,054.22 ± 2559.75	205,917.87 ± 10,633.49	166,937.98 ± 60.53.05	8508.80 ± 3385.86
Cd	mg/kg DW	<0.05	<0.05	<0.05–0.15	<0.05–0.21	<0.05–0.15	<0.05–0.10	<0.05–0.12	<0.05–0.21
Co	mg/kg DW	<0.05–0.19	<0.05–0.09	<0.05–6.55	<0.05–11.38	5.54 ± 0.72	1.31 ± 0.32	1.65 ± 0.18	6.39 ± 1.12
Cr	mg/kg DW	1.60 ± 0.67	1.84 ± 0.55	2.27 ± 1.30	14.43 ± 2.31	7.72 ± 0.70	5.82 ± 0.34	6.56 ± 0.36	10.15 ± 2.04
Cu	mg/kg DW	1.09 ± 0.10	1.16 ± 0.17	2.07 ± 1.24	10.80 ± 1.11	19.61 ± 2.56	6.77 ± 0.89	4.14 ± 0.28	6.54 ± 1.12
Fe	mg/kg DW	2876.30 ± 452.74	2111.37 ± 265.28	3388.53 ± 1789.84	24,898.91 ± 2669.90	16,619.55 ± 1432.00	14,148.77 ± 1040.91	19,779.71 ± 1436.96	9411.46 ± 1794.33
K	mg/kg DW	289.93 ± 63.90	336.49 ± 62.90	426.32 ± 209.48	747.79 ± 263.56	2736.89 ± 387.03	800.38 ± 67.78	548.69 ± 41.05	974.45 ± 259.07
Li	mg/kg DW	1.23 ± 0.20	1.15 ± 0.15	2.00 ± 1.10	7.86 ± 1.00	5.68 ± 0.21	3.53 ± 0.31	1.74 ± 0.08	5.49 ± 0.96
Mg	mg/kg DW	1533.07 ± 82.33	1442.17 ± 74.84	2628.05 ± 1078.12	7237.87 ± 1108.18	6343.99 ± 471.63	17,525.13 ± 1255.82	9680.30 ± 386.81	588.18 ± 68.45
Mn	mg/kg DW	66.39 ± 4.09	93.01 ± 10.30	115.78 ± 32.70	463.37 ± 51.01	325.64 ± 20.34	395.68 ± 27.68	367.01 ± 17.46	188.26 ± 23.14
Na	mg/kg DW	447.21 ± 20.51	290.17 ± 36.73	443.94 ± 95.75	403.75 ± 146.61	2638.86 ± 525.75	1315.91 ± 82.90	595.36 ± 17.87	282.94 ± 33.98
Ni	mg/kg DW	0.85 ± 0.23	0.70 ± 0.16	1.70 ± 1.39	14.85 ± 1.55	5.79 ± 0.19	6.04 ± 0.77	7.53 ± 0.60	6.95 ± 1.36
P	mg/kg DW	109.26 ± 7.57	149.74 ± 15.35	126.61 ± 15.84	216.46 ± 18.04	220.62 ± 11.86	519.64 ± 63.26	170.08 ± 9.49	64.95 ± 6.54
Pb	mg/kg DW	2.78 ± 0.10	4.07 ± 0.32	6.76 ± 1.76	27.57 ± 3.54	16.47 ± 1.62	14.27 ± 2.33	44.79 ± 2.78	0.94 ± 0.13
S	mg/kg DW	190.98 ± 12.31	141.60 ± 10.24	176.56 ± 7.91	102.77 ± 18.18	156.17 ± 42.60	1602.44 ± 73.73	598.32 ± 15.80	72.20 ± 9.67
Sr	mg/kg DW	296.35 ± 16.99	187.80 ± 6.86	201.49 ± 9.30	71.56 ± 17.22	102.74 ± 4.71	937.15 ± 73.68	890.88 ± 71.87	36.85 ± 12.15
V	mg/kg DW	6.28 ± 0.95	4.63 ± 0.74	4.69 ± 1.49	18.93 ± 2.11	46.76 ± 9.33	20.85 ± 1.18	19.26 ± 0.83	20.58 ± 4.86
Zn	mg/kg DW	3.32 ± 0.28	4.05 ± 0.81	9.24 ± 5.91	53.04 ± 6.74	35.58 ± 2.27	31.97 ± 3.20	83.47 ± 6.50	8.23 ± 1.60
N	mg/g DW	0.12 ± 0.02	0.24 ± 0.05	0.04 ± 0.01	0.12 ± 0.02	0.49 ± 0.19	0.53 ± 0.20	0.48 ± 0.09	0.13 ± 0.01

soil PC1 and PC3, indicating that the content of both phenolic compounds was higher in plants growing in soils with lower pH, Fe content and particle size, and higher microelement content. We found no significant associations between these seed chemical compounds and soil PC2. Similarly, there were no significant associations between total monoterpene content or individual compounds and any of the PCA axes.

4. Discussion

4.1. Soil properties and plant performance

The nutrient status of the soils supporting *C. maritimum* populations (represented by organic matter, macronutrient and microelement contents)

Table 2
Results of a Principal Component Analysis (PCA) summarizing the information of 8 soil physiochemical properties and concentrations of 21 mineral elements in the soil. Factor loadings, eigenvalues and % of variance explained of the first three principal components (PC1 soil, PC2 soil and PC3 soil) are shown. Values in bold show those factor loadings that represent the highest value on the three PCA components.

Variables	PC1 soil	PC2 soil	PC3 soil
Physicochemical properties			
Organic matter	−0.279	**0.525**	0.075
pH	0.063	0.124	**−0.403**
Conductivity	−0.542	−0.227	0.325
Coarse sand	**0.677**	0.210	−0.543
Fine sand	**−0.705**	0.050	0.505
Silt	**−0.685**	−0.234	0.395
Clay	−0.161	−0.372	**0.527**
Gravel	−0.488	−0.492	0.094
Mineral elements			
Al	−0.539	**−0.587**	0.079
As	−0.534	**0.721**	−0.059
B	−0.577	0.547	0.382
Ba	**−0.656**	−0.368	0.081
Ca	−0.352	**0.888**	0.090
Cr	**−0.705**	−0.400	−0.336
Cu	**−0.788**	−0.458	−0.118
Fe	**−0.800**	−0.055	**−0.562**
K	**−0.708**	−0.473	0.236
Li	**−0.709**	−0.494	−0.128
Mg	−0.673	**0.609**	−0.097
Mn	**−0.834**	0.112	−0.465
Na	**−0.627**	−0.092	0.317
Ni	**−0.749**	−0.229	−0.470
P	−0.593	**0.550**	0.230
Pb	**−0.564**	0.290	−0.532
S	−0.452	**0.776**	0.157
Sr	−0.307	**0.865**	0.086
V	**−0.743**	−0.329	−0.090
Zn	**−0.675**	0.243	−0.482
N	−0.385	**0.437**	0.272
Eigen value	10.516	6.292	3.180
% Variance explained	36.263	21.696	10.966

was highly variable across the study sites. However, concentrations of both N and P, generally the two most limiting macronutrients regulating plant growth and productivity in terrestrial ecosystems (Elser et al., 2007), were low compared to the average concentrations reported for soils by Markert (1992). Such low fertility is typical of sandy soils, mainly due to their low nutrient retention capacities (Cambrollé et al., 2015). The high salinities found in the soils are also noteworthy, since they could have crucial implications on the bioavailability and phytoaccumulation of mineral elements in this type of coastal ecosystems (Ondrasek and Rengel, 2021). Despite low N and P concentrations in the study populations, the GLMM revealed higher concentrations of both elements in leaves of *C. maritimum* plants growing in soils with lower organic matter content and macronutrient concentrations, including soil N and P (soil PC2). These results suggest that the N and P economies of *C. maritimum* leaves are regulated by demand rather than availability. Although there is generally a positive correlation between soil nutrient availability and tissue mineral content (Marschner, 1995), this is not a universal trend since plant nutritional requirements can be influenced by other factors, such as soil physical conditions or climate variations. N and P are tightly linked in plant metabolism (Wright et al., 2004). P uptake in plants is promoted under low N conditions (Kant et al., 2011), leading to a P accumulation in leaves (Schlüter et al., 2012). Moreover, P uptake was reported to be stimulated under low P conditions (Hermans et al., 2006), which in turn is active under low N conditions (Paul and Stitt, 1993). Our results support these observations, suggesting that similar mechanisms might occur in *C. maritimum*. In this context, it should be noted that halophytes have developed mechanisms for absorbing mineral nutrients in saline soils to avoid nutrient imbalances normally associated with salinity (Grattan and Grieve, 1992).

In addition, we found generally better plant performance under less fertile conditions, which has important implications for its cultivation in degraded soils. Specifically, our results indicated a greater plant volume and number of seeds in sandy soils with coarser texture and lower microelement content, and greater plant height in soils with lower organic matter and macronutrient content. Both vegetative growth and seed production are highly related to leaf N and P content, because of their central role in plant metabolism regulating growth and development (Elser et al., 2007; Ågren et al., 2012). Therefore, these results suggest that low N and P supply may be required to achieve optimum growth in *C. maritimum* plants in the field. In the line with these results, Labidi et al. (2011) reported greater relative growth of *C. maritimum* in response to P deprivation when plants were subjected to moderate saline concentration. These authors suggested that the tolerance of the species to P deprivation combined with moderate to high salinity is a behaviour which may explain the colonization of *C. maritimum* in habitats not suitable for other species, such as calcareous rocks or cliffs on seashores. However, Zenobi et al. (2022) reported the addition of N to the substrate produces plants with more leaf biomass. All these data suggest that *C. maritimum* is tolerant of mineral stress with physiological adaptations to avoid nutrient imbalances resulting from the disruption of mineral nutrient acquisition caused by salinity (Bloom et al., 1985). Hence, the higher growth under lower N and P concentrations could indicate that this species is able to grow where other species cannot thrive, as a refuge from interspecific competition for mineral resources. Likewise, the greater height and seed production in soils with lower microelement contents suggests that the demand for these mineral elements in *C. maritimum* is lower than their availability in the soils. The higher plant yield in soils with coarser texture could be related to the higher soil porosity, which significantly increases aeration (Deepagoda et al., 2011) and promotes gas exchange between the atmosphere and root environment, ultimately affecting plant growth and crop yield (Stepniewski et al., 1994; Mentges et al., 2016). In addition, soils with coarser texture typically have low water storage capacity, which in turn limits their fertility (Högberg and Högberg, 2002). However, the higher *C. maritimum* yield in soils with coarser texture could be related to adaptive physiological traits contributing to the tolerance of low water availability by halophytes, such as water storage in succulent leaves, efficient stomatal control and low transpiration rates (Marchesini et al., 2014). The absence of visible symptoms of nutrient deficiency in the field supports these ideas.

Overall, these data suggest the existence of adaptive mechanisms in *C. maritimum* to tolerate the nutrient limitations and high salt

Table 3
Linear mixed models (GLMM) testing the effects of soil factors affecting *C. maritimum* performance-related variables. Values indicate the *p*-value from GLMM, numerator degrees of freedom (NumDF) and denominator degrees of freedom (DenDF). Values in bold show significant associations between variables and the axis of soil PCA.

Variables	PC1 soil Texture + microelements				PC2 soil Organic matter + macronutrients				PC3 soil pH + clay + Fe			
	NumDF	DenDF	F	p	NumDF	DenDF	F	p	NumDF	DenDF	F	p
Plant volume	1	45.692	8.6592	**0.005097**	1	30.467	2.1264	0.155016	1	74.773	0.3462	0.558055
Vegetative height	1	48.938	1.9715	0.1666	1	32.441	4.7013	**0.03758**	1	77.209	0.257	0.61366
Number of infructescences	1	29.887	5.3787	**0.02741**	1	18.096	2.3326	0.14398	1	64.688	0.47	0.49542
Number of seeds/umbel	1	82.038	6.5017	**0.01264**	1	74.804	0.4631	0.49829	1	83.618	0.3148	0.57626
Number of seeds/plant	1	21.148	12.2907	**0.002087**	1	12.345	2.873	0.115133	1	54.968	0.0016	0.968025
Fruit weight	1	44.102	1.0707	0.30643	1	28.892	3.1735	0.08536	1	74.282	0.1269	0.72271
Seed weight	1	46.607	0.2523	0.6178	1	30.467	1.4304	0.2409	1	76.162	0.7366	0.3934

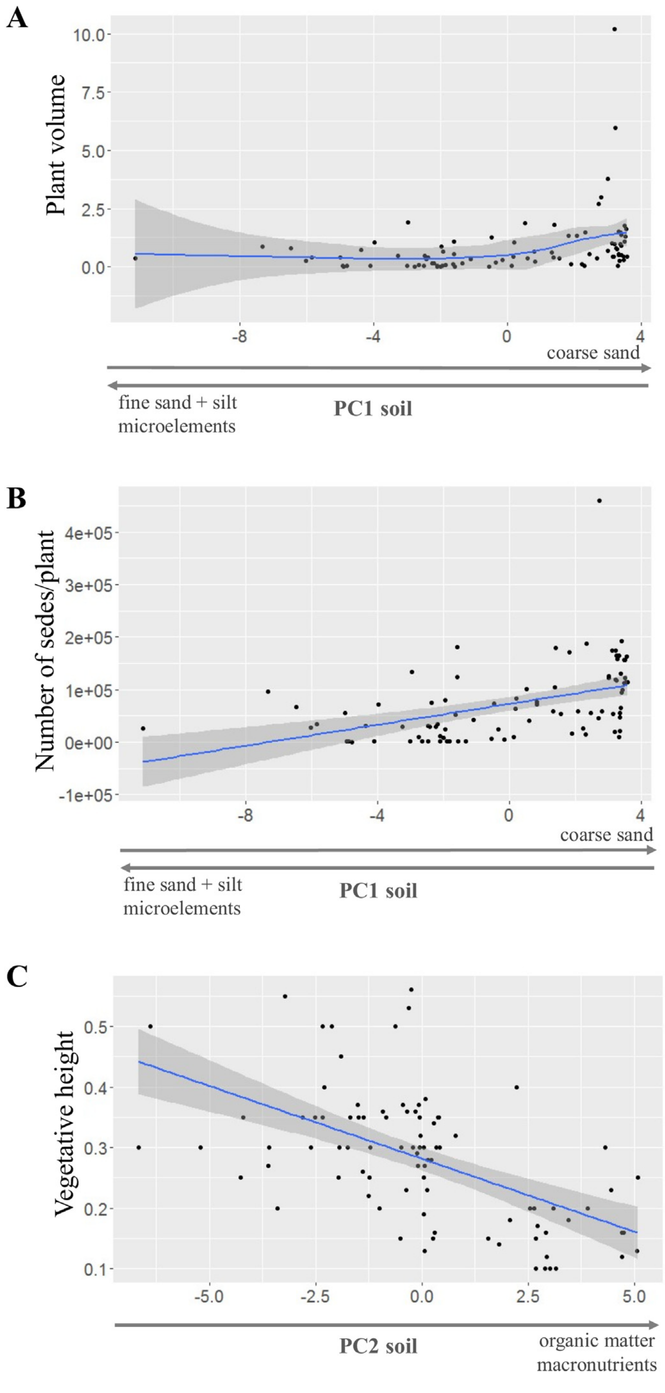


Fig. 2. Soil physicochemical properties associated with *Crithmum maritimum* performance. Significant relationships between soil physicochemical properties and plant performance variables: plant volume **(A)**, number of seeds per plant **(B)** and vegetative height **(C)**.

concentrations inherent in these environments, where other species cannot thrive; hence their exposure to interspecific competition is lower. Our results suggest that *C. maritimum* could be cultivated under low nutrient availability without impairing the yield of leaf biomass or seed production. It also shows that this species is highly appropriate for cultivation in saline or degraded soils that typically contain a low availability of essential elements. To develop sustainable cultivation practises, further studies under controlled greenhouse conditions should be performed to find threshold levels of nutrient deprivation that would not affect plant yield.

4.2. Soil properties and leaf nutritional traits

Our results showed that soil properties significantly influenced the metabolic profile of *C. maritimum* (Fig. 3). Particularly striking for leaves, were the significant associations of Na and Zn concentration with soil PC2 and PC3, respectively, revealed by GLMM. Higher Na content in plants growing in soils with lower organic matter and macronutrients concentration is consistent with previous studies reporting that the addition of organic matter in saline soils could potentially reduce Na plant uptake (Bello et al., 2021). Organic matter addition to saline soils improves porosity, hydraulic conductivity and permeability (Ondrasek and Rengel, 2021) and it can chelate cations, including Ca^{2+} and Mg^{2+}, thus favouring their plant uptake compared to Na^{+} (Bello et al., 2021). Na is an element that receives special attention in respect of halophyte crops, since the accumulation of Na in their edible parts is one of the main concerns for human consumption. Although Na is essential in the human diet, its excessive intake is related to an increase in blood pressure, which represents a risk factor for cardiovascular disease (Mozaffarian et al., 2014). Hence, the addition of organic matter and macronutrients to the soil might be used to minimize the uptake of Na in *C. maritimum,* thus enabling greater consumption.

On the other hand, we detected higher leaf Zn content in plants growing in soils with lower pH and Fe concentrations and higher clay content. Zn is an essential micronutrient for plant growth and development and it is well-known that its availability is controlled by both soil properties and biological factors (Hacisalihoglu and Kochian, 2003). Zn availability for plants decreases as soil pH increases (Marschner, 1995) and Fe oxides adsorb Zn through surface complexation in a process dependent on pH (Stahl and James, 1991; Ryan et al., 2013). In addition, it is known that clay soils have a higher Zn adsorption and retention capacity than other soils (especially sandy ones) and clay minerals have been described as the main Zn-sorbent surfaces in soils (González-Costa et al., 2017). Thus, the content of Zn in *C. maritimum* leaves could be increased by manipulating soil properties (pH, Fe and clay content) by affecting its bioavailability. This is particularly interesting since Zn is an essential trace element for humans and its deficiency is a widespread nutritional problem (Alloway, 2009).

Leaf protein content was higher in *C. maritimum* plants growing in soils of lower fertility (i.e. with lower organic matter and macronutrients including Mg, P, S and N). Although this finding may be unexpected, since carbon and N are primary components of amino acids and protein synthesis, their availability should stimulate synthesis (Nunes-Nesi et al., 2010), and variable responses of plant protein metabolism have been described within species under low nutrient availability. For example, Lu and Zhang (2000) reported that maize plants save N by reducing synthesis of proteins under low nutrient supply (mainly N), whereas an up-regulation in protein metabolism in the same species was reported under N depletion (Schlüter et al., 2013). Furthermore, the availability of other minerals, such as Mg, as well as interactions between different macronutrients, can affect protein metabolism positively or negatively in plant leaves (Sun et al., 2018). Given the low nutrient content in the soils of the study areas, our results suggest that high protein yields could be obtained in *C. maritimum* without need of applying fertilizers, which is particularly significant for its cultivation in marginal environments with poor soil conditions.

Lipids are other compounds of high nutritional value and bioactivity in halophytes (Maciel et al., 2018). The absence of relationships between lipid content and fatty acid composition and the PCA axes suggest that the soil properties here analysed do not strongly affect the lipid biosynthesis in *C. maritimum* leaves, unlike some other plants (Gaude et al., 2007) including other edible halophytes (Custódio et al., 2020). However, we have previously reported that *C. maritimum* plants exhibit a lipid composition healthier for consumption, mainly due to a higher PUFA content, when they are grown under non-limiting nutrient conditions in absence of stressors, in comparison with wild plants (Martins-Noguerol et al., 2022b). In the light of these findings, other abiotic factors should be explored in order to optimize the lipid yield in *C. maritimum* leaves and to produce plants with a healthier lipid profile.

Table 4
Linear mixed models (GLMM) testing the effects of soil factors affecting *C. maritimum* leaf traits. Values indicate the p-value from GLMM, numerator degrees of freedom (NumDF) and denominator degrees of freedom (DenDF). Values in bold show significant associations between variables and the axis of soil PCA. MUFA: monounsaturated fatty acids; PUFA: polyunsaturated fatty acids; TPC: total phenolic content.

Variables	PC1 soil Texture + microelements				PC2 soil Organic matter + macronutrients				PC3 soil pH + clay + Fe			
	NumDF	DenDF	F	p	NumDF	DenDF	F	p	NumDF	DenDF	F	p
Protein												
Protein content	1	77.349	0.0033	0.9540	1	**78.588**	**5.1162**	**0.0265**	1	82.815	15.2080	0.2210
Lipids												
Lipid content	1	59.301	0.3361	0.5643	1	42.633	0.1792	0.6742	1	78.701	0.0728	0.7800
MUFA	1	72.949	1.2807	0.2615	1	68.132	0.0298	0.8633	1	73.301	2.0473	0.1567
PUFA	1	66.815	0.4872	0.4876	1	55.569	0.7513	0.3898	1	73.999	0.1471	0.7024
PUFA/SFA	1	51.513	0.9661	0.3303	1	37.602	1.9085	0.1753	1	71.121	2.5773	0.1128
Atherogenic index	1	62.454	0.4654	0.4976	1	50.054	0.7158	0.4016	1	73.567	0.9292	0.3382
Thrombogenic index	1	47.005	0.5313	0.4697	1	33.639	1.5772	0.2178	1	69.216	1.8410	0.1792
Minerals												
Ca	1	38.725	3.0013	0.0912	1	39.709	0.9001	0.3484	1	66.302	0.0389	0.8442
K	1	18.311	2.6461	0.1209	1	17.535	2.6402	0.1220	1	44.366	0.0984	0.7552
Mg	1	38.795	0.0834	0.7742	1	39.856	0.0241	0.8775	1	66.449	0.8328	0.3648
Na	1	24.349	0.4432	0.5118	1	**23.667**	**5.0669**	**0.0340**	1	52.285	0.0033	0.9547
P	1	30.62	0.0833	0.7749	1	**30.478**	**4.9209**	**0.0341**	1	59.0170	0.0118	0.9140
S	1	36.577	0.2693	0.6069	1	37.148	0.9156	0.3448	1	64.379	0.1141	0.7366
N	1	78.222	0.0036	0.9520	1	**79.347**	**4.7694**	**0.0319**	1	82.907	0.8758	0.3521
Cu	1	35.954	0.0001	0.9918	1	36.708	1.9441	0.1716	1	64.145	0.4507	0.5044
Mn	1	22.02	0.8197	0.3751	1	21.14	1.4843	0.2365	1	49.33	2.3689	0.1302
Zn	1	17.354	0.6731	0.4231	1	16.147	3.2105	0.0919	1	**42.422**	**4.1900**	**0.0469**
Cr	1	26.387	0.7184	0.4043	1	26.093	0.2887	0.5956	1	54.830	0.4731	0.4945
Ni	1	20.684	0.0482	0.8283	1	19.549	0.9292	0.3468	1	47.361	0.8833	0.3521
Bo	1	44.81	0.5150	0.4767	1	46.084	0.6665	0.4185	1	70.229	1.0553	0.3078
Fe	1	64.341	1.1446	0.2887	1	66.343	0.4045	0.5270	1	79.597	0.4331	0.5124
Phenolics												
TPC	1	59.468	0.1799	0.6730	1	**42.869**	**9.7114**	**0.0033**	1	80.588	0.3607	0.5498
Flavonoids content	1	61.568	0.3880	0.5357	1	**45.132**	**8.9470**	**0.0045**	1	81.165	0.1388	0.7105
Hydroxycinnamic acids content	1	23.978	0.1000	0.7546	1	15.018	3.2340	0.0923	1	**55.382**	**4.5765**	**0.0368**
Terpenes												
Monoterpenes content	1	68.27	0.6780	0.4131	1	57.682	3.6695	0.0604	1	78.000	1.8155	0.1818
sabinene	1	66.27	0.3600	0.5506	1	55.071	3.6694	0.0606	1	77.966	0.0000	0.9958
p-cymene	1	**69.63**	**5.0249**	**0.0282**	1	59.782	3.3171	0.0736	1	77.99	2.0497	0.1562
γ-terpinene	1	13.666	1.4594	0.2475	1	9.235	2.1586	0.1750	1	48.469	0.3966	0.5318
thymol methyl ether	1	51.09	0.0914	0.7636	1	**38.171**	**7.2247**	**0.0106**	1	76.302	0.1899	0.6642

Table 5
Linear mixed models (GLMM) testing the effects of soil factors affecting *C. maritimum* seed traits. Values indicate the p-value from GLMM, numerator degrees of freedom (NumDF) and denominator degrees of freedom (DenDF). Values in bold show significant associations between variables and the axis of soil PCA. MUFA: monounsaturated fatty acids; PUFA: polyunsaturated fatty acids; TPC: total phenolic content.

Variables	PC1 soil Texture + microelements				PC2 soil Organic matter + macronutrients				PC3 soil pH + clay + Fe			
	NumDF	DenDF	F	p	NumDF	DenDF	F	p	NumDF	DenDF	F	p
Oil content												
Oil content	1	35.405	0.0412	0.8403	1	24.547	1.4106	0.2463	1	62.964	0.7173	0.4002
Atherogenic index	1	**76.197**	**8.202**	**0.005403**	1	76.972	0.1213	0.728573	1	74.205	0.1588	0.691414
Thrombogenic index	1	**62.646**	**5.2255**	**0.02565**	1	50.287	0.3639	0.54906	1	75.54	0.0002	0.99011
PUFA/SFA	1	**34.629**	**10.8415**	**0.002292**	1	25.483	0.0051	0.943709	1	60.01	0.8789	0.352252
MUFA	1	55.516	0.3474	0.558	1	41.288	0.6434	0.4271	1	74.138	0.6905	0.4087
PUFA	1	**24.229**	**6.0048**	**0.02186**	1	17.981	0.0148	0.9045	1	47.338	1.6038	0.21156
Phenolics												
TPC	1	40.495	1.4459	0.2362	1	41.712	1.1572	0.2882	1	59.279	2.4865	0.1202
3-Caffeoyl quinic acid	1	43.487	0.4348	0.51313	1	44.874	2.8037	0.10101	1	**60.991**	**4.3131**	**0.04204**
5-Caffeoyl quinic acid	1	32.56	0.9512	0.33661	1	31.312	2.0027	0.16689	1	**53.057**	**6.2599**	**0.01547**
p-Coumaroyl quinic acid	1	21.03	3.1287	0.09143	1	18.157	0.0179	0.89497	1	41.493	2.2068	0.14496
Feruloyl quinic acid	1	**25.186**	**4.5387**	**0.043081**	1	23.88	1.9047	0.180333	1	**46.61**	**7.8075**	**0.007528**
Ferulic acid	1	52.773	1.282	0.2627	1	55.341	0.5768	0.4508	1	65.938	1.938	0.1689
3,5-Dicaffeoylquinic acid	1	11.1559	0.2192	0.6487	1	8.8249	0.2904	0.60327	1	**26.941**	**7.2188**	**0.01221**
4,5-Dicaffeoylquinic acid	1	29.285	0.1522	0.6993	1	28.138	3.812	0.0609	1	**50.45**	**6.0359**	**0.0175**
Quercetin-O-hexoside	1	42.745	0.786	0.3803	1	43.796	0.1175	0.7334	1	60.44	0.6429	0.4258
Quercetin-7-xyloside	1	**14.5653**	**14.319**	**0.001888**	1	8.9264	1.02	0.3391065	1	**31.0313**	**18.237**	**0.0001711**
Chrysoeriol-7-O-neohesperidoside	1	31.318	1.3589	0.2525	1	31.963	1.0307	0.3176	1	52.916	2.3766	0.1291

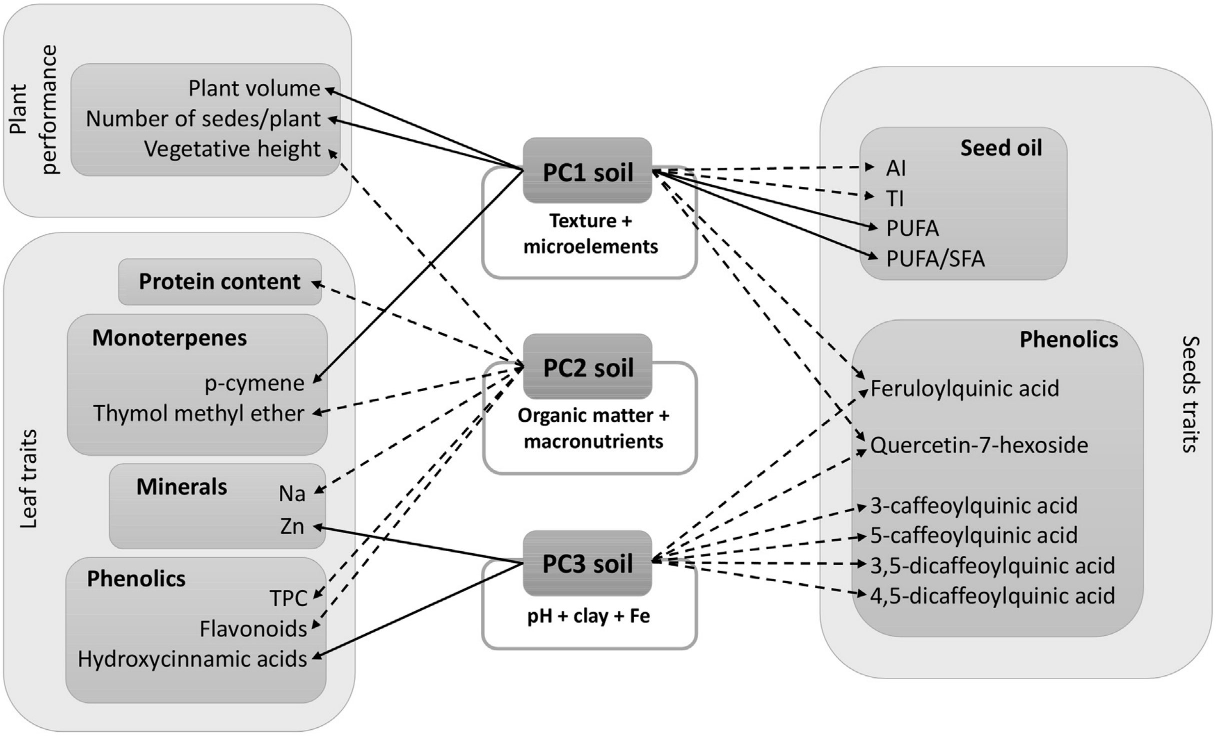


Fig. 3. Soil physicochemical properties associated with *Crithmum maritimum* yield. Diagram shows significant associations between soil physicochemical properties and plant performance, leaf and seed traits in *C. maritimum* derived from the generalized linear mixed model analyses. PC1 soil, PC2 soil and PC3 soil summarize a suite of soil variables associated with physicochemical properties, macronutrients and microelements from the soil PCA (*see statistical analyses*). Continuous arrows indicate significant positive associations whereas dashed arrows represent significant negative associations.

4.3. Soil properties and leaf secondary metabolites

We report for the first time significant associations between phenolic content and some soil physicochemical properties in this species (Fig. 3). TPC and flavonoid content (the dominant compounds detected in *C. maritimum* leaves) were higher in plants growing in less fertile soils. According to the carbon-nutrient balance hypothesis, the concentration of phenolic compounds, which are carbon-based defences against abiotic and biotic constraints, should increase in nutrient-poor environments and decrease in nutrient-rich environments (Bryant et al., 1983), which is consistent with our results. An increase of flavonoid concentration in response to nutrient limitation, particularly N and P, has been well documented (Stewart et al., 2001; Lea et al., 2007). Therefore, the depletion of macronutrients such as N and P, and organic matter content could be an interesting and economically feasible strategy to produce *C. maritimum* plants with higher polyphenol content. In fact, manipulation of macronutrient concentration has already been reported as a method to modify the levels of these desirable compounds and improve plant quality (Lillo et al., 2008). Besides flavonoids, we detected between 11.9 and 21.7 % of hydroxycinnamic acids (Supplementary Table 2) in contrast to previous work, where these metabolites were the dominant compounds in the polyphenol profile of *C. maritimum* plants collected in western France and northern Spain (Meot-Duros and Magné, 2009; Sánchez-Faure et al., 2020). This could be attributed to singularities in the physiology of different genotypes. Although other genetic and abiotic elements should be examined to find the main factors determining the dominance of these metabolites, our results suggest that specific soil physical and chemical factors, including pH, clay and soil Fe content, could also influence their biosynthesis and accumulation.

On the other hand, we also found several soil abiotic properties that could influence the content of specific monoterpenes. Particularly, we found that lower levels of soil organic matter and macronutrient content could promote a greater accumulation of thymol methyl ether, whereas a coarser texture and lower microelements content could foster a higher accumulation of p-cymene, another abundant monoterpene in *C. maritimum* leaves from Mediterranean accessions (Supplementary Table 1). Monoterpenes are the main constituents of an essential oil in *C. maritimum* that has different potential applications, such as the production of insecticides (Suresh et al., 2020). However, depending on the relative abundance of these compounds in the essential oil, different chemotypes with individual potential applications can be found in this species (Pavela et al., 2017; Suresh et al., 2020). Thymol methyl ether is the aromatic monoterpenoid predominant in Mediterranean *C. maritimum* populations (Pavela et al., 2017), which is consistent with our findings since this compound was the most represented in leaves from all the study populations (Supplementary Table 1). Monoterpenoids are known components of plant defence responses to abiotic and biotic stresses and their content can be influenced by both factors, as well as by the life-cycle stage of the plant (Renna, 2018). Furthermore, we found for the first time that soil factors can affect the content of specific monoterpenes, informing future studies focussed on essential oil in this species.

4.4. Soil properties and seed traits

Despite the oil content of *C. maritimum* seeds not being significantly associated with soil PCA axes, soil properties significantly influenced the nutritional oil composition (Fig. 3). Thus, we found higher PUFA percentages on soils with coarser texture and lower microelement contents, which was reflected in a higher PUFA/SFA ratio and lower AI and TI indexes. Higher PUFA content and PUFA/SFA ratio are desirable from a human health perspective, since they have been largely associated with beneficial effects and some of them contain essential fatty acids that must be acquired through the diet (Simopoulos, 2011). On the other hand, the consumption of lipids with lower AI and TI indexes are related with reduced risk of coronary heart disease (Chen and Liu, 2020). It is well established that plant lipid biosynthesis is influenced by multiple environmental factors including soil nutrients (Singer et al., 2016; Hodges, 2010). However, the contribution of specific minerals can be different depending on the plant species. N, K and Mg were related to high seed and oil yields (Bellaloui et al., 2018; Wacal et al., 2019) whereas S and Mn deficiencies can affect the seed oil quantity and quality negatively (Wilson et al., 1982; D'Hooghe et al., 2014). Our work suggests that the nutritional quality of *C. maritimum* seed oil could be enhanced by manipulating the availability of microelements, although additional studies are needed to find threshold concentrations.

We also found that a lower clay percentage and higher pH and Fe content was related to seeds with higher content of chlorogenic acid isomers (namely 3-caffeoylquinic acid, 5-caffeoylquinic acid, 3,5-dicaffeoylquinic acid, 4,5-dicaffeoylquinic acid and feruloyl quinic acid). Furthermore, feruloyl quinic acid and quercetin-7-hexoside were also related to soil texture and macronutrients. It is well known that phenolic compounds are plastically generated by plants in response to environmental conditions, apart from genetic factors (Brunetti et al., 2018). However, the increase in phenolics can be influenced by different soil factors, such as pH or mineral elements, depending on the plant species (e.g. Chen et al., 2020; Klimienė et al., 2021). Our results suggest that *C. maritimum* seeds display higher content of chlorogenic isomers in soils with lower clay content and higher pH and Fe concentration, which is a useful insight for commercial cultivation since these metabolites are highly appreciated in nutraceutical industry, because of their biological properties, including antibacterial, anti-inflammatory and antioxidant characteristics (Liang and Kitts, 2016).

5. Conclusions

This is the first study to analyse the influence of soil factors, including a wide range of physicochemical properties, on yield and phytochemical traits in the edible halophyte *Crithmum maritimum*. Our findings suggest that this species is potentially suitable to be cultivated in underutilized, poor-nutrient soils, due to its ability to maintain growth performance and the production of phytochemical constituents across a wide array of environmental conditions. Moreover, our results indicate that *C. maritimum* maximizes the accumulation of protein and phenolics (including flavonoids) in leaves under low nutrient supply (organic matter and macronutrients), although these conditions could also increase Na uptake. Another benefit, improved nutritional quality of the seed oil could be related to coarser texture and lower microelement contents in the soil. This synthesis reveals new opportunities for the exploitation of *C. maritimum* in sustainable agriculture, particularly for cultivation on degraded lands with low levels of nutrients and high salinities.

CRediT authorship contribution statement

Raquel Martins-Noguerol: Data curation, Investigation, Methodology, Visualization, Supervision, Writing – original draft, Writing – review & editing. **Luis Matías:** Formal analysis, Investigation, Methodology, Software, Supervision, Validation, Writing – review & editing. **Ignacio M. Pérez-Ramos:** Formal analysis, Investigation, Methodology, Software, Supervision, Validation, Writing – review & editing. **Xoaquín Moreira:** Funding acquisition, Methodology, Resources, Supervision, Validation, Writing – review & editing. **Marta Francisco:** Investigation. **Justo Pedroche:** Investigation, Resources. **Cristina DeAndrés-Gil:** Investigation. **Eduardo Gutiérrez:** Investigation. **Joaquín J. Salas:** Investigation, Resources. **Antonio J. Moreno-Pérez:** Investigation, Supervision, Writing – review & editing. **Anthony J. Davy:** Supervision, Writing – review & editing. **Sara Muñoz-Vallés:** Investigation, Methodology. **Manuel Enrique Figueroa:** Supervision, Writing – review & editing. **Jesús Cambrollé:** Conceptualization, Funding acquisition, Resources, Project administration, Methodology, Supervision, Validation, Writing – review & editing.

Data availability

Data will be made available on request.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Acknowledgements

We thank the Agencia Estatal de Investigación (AEI) and the Spanish Science and Innovation Ministry for financial support to the projects RTI2018-099260-A-I00 (J. Cambrollé) and RTI2018-099322-B-100 (X. Moreira). R. Martins-Noguerol was financially supported by the Spanish Universities Ministry and European Union - Next Generation EU. We also thank to Alberto García-González for his help during field sampling and plant measurements.

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.scitotenv.2023.161806.

References

Ågren, G.I., Wetterstedt, J.M., Billberger, M.F., 2012. Nutrient limitation on terrestrial plant growth–modeling the interaction between nitrogen and phosphorus. New Phytol. 194 (4), 953–960. https://doi.org/10.1111/j.1469-8137.2012.04116.x.

Agudelo, A., Carvajal, M., Martinez-Ballesta, M.D.C., 2021. Halophytes of the Mediterranean basin-underutilized species with the potential to be nutritious crops in the scenario of the climate change. Foods 10 (1), 119. https://doi.org/10.3390/foods10010119.

Akula, R., Ravishankar, G.A., 2011. Influence of abiotic stress signals on secondary metabolites in plants. Plant Signal. Behav. 6 (11), 1720–1731. https://doi.org/10.4161/psb.6.11.17613.

Alloway, B.J., 2009. Soil factors associated with zinc deficiency in crops and humans. Environ. Geochem. Health 31 (5), 537–548. https://doi.org/10.1007/s10653-009-9255-4.

Atia, A., Barhoumi, Z., Mokded, R., Abdelly, C., Smaoui, A., 2011. Environmental ecophysiology and economical potential of the halophyte crithmum maritimum L (Apiaceae). J. Med. Plant Res. 5 (16), 3564–3571.

Barton, K., 2009. MuMIn: Multi-model Inference. . http://r-forge.r-project.org/projects/mumin/.

Bates, D., Maechler, M., Bolker, B., Walker, S., 2015. Fitting linear mixed effects models using lme4. J. Stat. Softw. 67, 1–48. https://doi.org/10.18637/jss.v067.i01.

Bellaloui, N., Abbas, H.K., Ebelhar, M.W., Mengistu, A., Mulvaney, M.J., Accinelli, C., Shier, W.T., 2018. Effect of increased nitrogen application rates and environment on protein, oil, fatty acids, and minerals in sesame (Sesamum indicum) seed grown under Mississippi Delta conditions. Food Nutr. Sci. 9 (09), 1115. https://doi.org/10.4236/fns.2018.99081.

Bello, S.K., Alayafi, A.H., AL-Solaimani, S.G., Abo-Elyousr, K.A., 2021. Mitigating soil salinity stress with gypsum and bio-organic amendments: a review. Agronomy 11 (9), 1735. https://doi.org/10.3390/agronomy11091735.

Bloom, A.J., Chapin, F.S., Mooney, H.A., 1985. Resource limitation in plants–an economic analogy. Annu. Rev. Ecol. Syst., 363–392.. https://www.jstor.org/stable/2097053.

Bouyoucos, G.J., 1962. Hydrometer method improved for marking partied size analyses of soil. Agron. J. 54, 464–465. https://doi.org/10.2134/agronj1962.00021962005400050028x.

Brunetti, C., Fini, A., Sebastiani, F., Gori, A., Tattini, M., 2018. Modulation of phytohormone signaling: a primary function of flavonoids in plant–environment interactions. Front. Plant Sci. 9, 1042. https://doi.org/10.3389/fpls.2018.01042.

Bryant, J.P., Chapin III, F.S., Klein, D.R., 1983. Carbon/nutrient balance of boreal plants in relation to vertebrate herbivory. Oikos 357–368.

Cambrollé, J., Muñoz-Vallés, S., Mancilla-Leytón, J.M., Andrades-Moreno, L., Luque, T., Figueroa, M.E., 2015. Effects of soil physicochemical properties on plant performance of Glaucium flavum crantz. Plant Soil 386 (1), 185–193. https://doi.org/10.1007/s11104-014-2258-7.

Castillo, J.M., Mancilla-Leytón, J.M., Martins-Noguerol, R., Moreira, X., Moreno-Pérez, A.J., Muñoz-Vallés, S., Pedroche, J., Figueroa, M.E., García-González, A., Salas, J.J., Millán-Linares, M.C., Francisco, M., Cambrollé, J., 2022. Interactive effects between salinity and nutrient deficiency on biomass production and bio-active compounds accumulation in the halophyte crithmum maritimum. Sci. Hortic. 301, 111136. https://doi.org/10.1016/j.scienta.2022.111136.

Chen, J., Liu, H., 2020. Nutritional indices for assessing fatty acids: a mini-review. Int. J. Mol. Sci. 21 (16), 5695. https://doi.org/10.3390/ijms21165695.

Chen, L., Xia, F., Wang, M., Wang, W., Mao, P., 2020. Metabolomic analyses of alfalfa (Medicago sativa L. Cv. 'Aohan') reproductive organs under boron deficiency and surplus conditions. Ecotoxicol. Environ. Saf. 202, 111011. https://doi.org/10.1016/j.ecoenv.2020.111011.

Cunsolo, F., Ruberto, G., Amico, V., Piatelli, M., 1993. Bioactive metabolites from sicilian marine fennel, Crithmum maritimum. J. Nat. Prod. 56, 1598–1600. https://doi.org/10.1021/np50099a022.

Custódio, M., Maciel, E., Domingues, M.R., Lillebø, A.I., Calado, R., 2020. Nutrient availability affects the polar lipidome of Halimione portulacoides leaves cultured in hydroponics. Sci. Rep. 10 (1), 1–13. https://doi.org/10.1038/s41598-020-63551-1.

Deepagoda, T.C., Moldrup, P., Schjønning, P., Jonge, L.W.D., Kawamoto, K., Komatsu, T., 2011. Density-corrected models for gas diffusivity and air permeability in unsaturated soil. Vadose Zone J. 10 (1), 226–238. https://doi.org/10.2136/vzj2009.0137.

D'Hooghe, P., Dubousset, L., Gallardo, K., Kopriva, S., Avice, J.C., Trouverie, J., 2014. Evidence for proteomic and metabolic adaptations associated with alterations of seed yield and quality in sulfur-limited Brassica napus L. MPC 13 (5), 1165–1183. https://doi.org/10.1074/mcp.M113.034215.

Elser, J.J., Bracken, M.E., Cleland, E.E., Gruner, D.S., Harpole, W.S., Hillebrand, H., Ngai, J.T., Seabloom, E.W., Shurin, J.B., Smith, J.E., 2007. Global analysis of nitrogen and phosphorus limitation of primary producers in freshwater, marine and terrestrial ecosystems. Ecol. Lett. 10 (12), 1135–1142. https://doi.org/10.1111/j.1461-0248.2007.01113.x.

Garcés, R., Mancha, M., 1993. One-step lipid extraction and fatty acid methyl esters preparation from fresh plant tissues. Anal. Biochem. 211 (1), 139–143. https://doi.org/10.1006/abio.1993.1244.

Gaude, N., Bréhélin, C., Tischendorf, G., Kessler, F., Dörmann, P., 2007. Nitrogen deficiency in Arabidopsis affects galactolipid composition and gene expression and results in accumulation of fatty acid phytyl esters. Plant J. 49 (4), 729–739. https://doi.org/10.1111/j.1365-313X.2006.02992.x.

Gil, R., Bautista, I., Boscaiu, M., Lidón, A., Wankhade, S., Sánchez, H., Llinares, J., Vicente, O., 2014. Responses of five Mediterranean halophytes to seasonal changes in environmental conditions. AoB Plants 6. https://doi.org/10.1093/aobpla/plu049.

González-Costa, J.J., Reigosa, M.J., Matías, J.M., Fernández-Covelo, E., 2017. Analysis of the importance of oxides and clays in cd, cr, cu, ni, pb and zn adsorption and retention with regression trees. PloS ONE 12 (1), e0168523. https://doi.org/10.1371/journal.pone.0168523.

Grattan, S.R., Grieve, C.M., 1992. Mineral element acquisition and growth response of plants grown in saline environments. Agric. Ecosyst. Environ. 38 (4), 275–300. https://doi.org/10.1016/0167-8809(92)90151-Z.

Griesser, M., Weingart, G., Schoedl-Hummel, K., Neumann, N., Becker, M., Varmuza, K., Liebner, F., Schuhmacher, R., Forneck, A., 2015. Severe drought stress is affecting selected primary metabolites, polyphenols, and volatile metabolites in grapevine leaves (Vitis vinifera cv. Pinot noir). Plant Physiol. Biochem. 88, 17–26. https://doi.org/10.1016/j.plaphy.2015.01.004.

Hacisalihoglu, G., Kochian, L.V., 2003. How do some plants tolerate low levels of soil zinc? Mechanisms of zinc efficiency in crop plants. New Phytol. 159 (2), 341–350. https://doi.org/10.1046/j.1469-8137.2003.00826.x.

Hara, A., Radin, N.S., 1978. Lipid extraction of tissues with a low-toxicity solvent. Anal. Biochem. 90 (1), 420–426. https://doi.org/10.1016/0003-2697(78)90046-5.

Hermans, C., Hammond, J.P., White, P.J., Verbruggen, N., 2006. How do plants respond to nutrient shortage by biomass allocation? Trends Plant Sci. 11 (12), 610–617. https://doi.org/10.1016/j.tplants.2006.10.007.

Hodges, S.C., 2010. Soil Fertility Basics; Soil Science Extension. North Carolina State University, Raleigh, NC, USA, pp. 1–75.

Högberg, M.N., Högberg, P., 2002. Extramatrical ectomycorrhizal mycelium contributes one-third of microbial biomass and produces, together with associated roots, half the dissolved organic carbon in a forest soil. New Phytol. 154 (3), 791–795. https://doi.org/10.1046/j.1469-8137.2002.00417.x.

Kant, S., Peng, M., Rothstein, S.J., 2011. Genetic regulation by NLA and microRNA827 for maintaining nitrate-dependent phosphate homeostasis in arabidopsis. PLoS Genet. 7 (3), e1002021. https://doi.org/10.1371/journal.pgen.1002021.

Karkanis, A., Polyzos, N., Kompocholi, M., Petropoulos, S.A., 2022. Rock samphire, a candidate crop for saline agriculture: cropping practices, chemical composition and health effects. Appl. Sci. 12 (2), 737. https://doi.org/10.3390/app12020737.

Kjeldahl, J., 1883. A new method for the determination of nitrogen in organic matter. Z. Anal. Chem. 22, 366–382. https://doi.org/10.1007/BF01338151.

Klimienė, A., Klimas, R., Shutava, H., Razmuvienė, L., 2021. Dependence of the concentration of bioactive compounds in Origanum vulgare on chemical properties of the soil. Plants 10 (4), 750. https://doi.org/10.3390/plants10040750.

Labidi, N., Ammari, M., Snoussi, S., Messelini, N., Gharbi, F., Abdelly, C., 2011. Stimulated growth rate by restriction of P availability at moderate salinity but insensitive to P availability at high salinity in Crithmum maritimum. Acta Biol. Hung. 62 (3), 302–315. https://doi.org/10.1556/ABiol.62.2011.3.9.

Lea, U.S., Slimestad, R., Smedvig, P., Lillo, C., 2007. Nitrogen deficiency enhances expression of specific MYB and bHLH transcription factors and accumulation of end products in the flavonoid pathway. Planta 225 (5), 1245–1253. https://doi.org/10.1007/s00425-006-0414-x.

Liang, N., Kitts, D.D., 2016. Role of chlorogenic acids in controlling oxidative and inflammatory stress conditions. Nutrients 8 (1), 16. https://doi.org/10.3390/nu8010016.

Lillo, C., Lea, U.S., Ruoff, P., 2008. Nutrient depletion as a key factor for manipulating gene expression and product formation in different branches of the flavonoid pathway. Plant Cell Environ. 31 (5), 587–601. https://doi.org/10.1111/j.1365-3040.2007.01748.x.

Lokhande, V.H., Suprasanna, P., 2012. Prospects of halophytes in understanding and managing abiotic stress tolerance. In: Ahmad, P., Prasad, M.N.V. (Eds.), Environmental Adaptations and Stress Tolerance of Plants in the Era of Climate Change. Springer, New York, pp. 29–56.

Lopes, M., Sanches-Silva, A., Castilho, M., Cavaleiro, C., Ramos, F., 2021. Halophytes as source of bioactive phenolic compounds and their potential applications. Crit. Rev. Food Sci. Nutr. 1–24. https://doi.org/10.1080/10408398.2021.1959295.

Lu, C., Zhang, J., 2000. Photosynthetic CO2 assimilation, chlorophyll fluorescence and photoinhibition as affected by nitrogen deficiency in maize plants. Plant Sci. 151 (2), 135–143. https://doi.org/10.1016/S0168-9452(99)00207-1.

Maciel, E., Lillebø, A., Domingues, P., da Costa, E., Calado, R., Domingues, M.R.M., 2018. Polar lipidome profiling of Salicornia ramosissima and Halimione portulacoides and the relevance of lipidomics for the valorization of halophytes. Phytochemistry 153, 94–101. https://doi.org/10.1016/j.phytochem.2018.05.015.

Marchesini, V.A., Yin, C., Colmer, T.D., Veneklaas, E.J., 2014. Drought tolerances of three stem-succulent halophyte species of an inland semiarid salt lake system. Funct. Plant Biol. 41 (12), 1230–1238. https://doi.org/10.1071/FP14108.

Markert, B., 1992. Presence and significance of naturally occurring chemical elements of the periodic system in the plant organism and consequences for future investigations on inorganic environmental chemistry in ecosystems. Vegetatio 103 (1), 1–30. https://doi.org/10.1007/BF00033413.

Marschner, H., 1995. Mineral Nutrition of Higher Plants. 2nd edn. Academic Press, London.

Martins-Noguerol, R., Pérez-Ramos, I.M., Matías, L., Moreira, X., Francisco, M., García-González, A., Troncoso-Ponce, M.A., Thomasset, B., Martínez-Force, E., Moreno-Pérez, A.J., Cambrollé, J., 2022a. Crithmum maritimum seeds, a potential source for high-quality oil and phenolic compounds in soils with no agronomical relevance. J. Food Compos. Anal. 104413. https://doi.org/10.1016/j.jfca.2022.104413.

Martins-Noguerol, R., Matías, L., Pérez-Ramos, I.M., Moreira, X., Muñoz-Vallés, S., Mancilla-Leytón, J.M., Francisco, M., García-González, A., DeAndrés-Gil, C., Martínez-Force, E., Millán-Linares, M.C., Pedroche, J., Figueroa, M.E., Moreno-Pérez, A.J., Cambrollé, J., 2022b. Differences in nutrient composition of sea fennel (Crithmum maritimum) grown in different habitats and optimally controlled growing conditions. J. Food Compos. Anal. 104266. https://doi.org/10.1016/j.jfca.2021.104266.

Mentges, M.I., Reichert, J.M., Rodrigues, M.F., Awe, G.O., Mentges, L.R., 2016. Capacity and intensity soil aeration properties affected by granulometry, moisture, and structure in no-tillage soils. Geoderma 263, 47–59. https://doi.org/10.1016/j.geoderma.2015.08.042.

Meot-Duros, L., Magné, C., 2009. Antioxidant activity and phenol content of crithmum maritimum L. Leaves. Plant Physiol. Biochem. 47 (1), 37–41. https://doi.org/10.1016/j.plaphy.2008.09.006.

Moreira, X., Pérez-Ramos, I.M., Matías, L., Francisco, M., García-González, A., Martins-Noguerol, R., Vázquez-González, C., Abdala-Roberts, L., Cambrollé, J., 2021. Effects of soil abiotic factors and plant chemical defences on seed predation on sea fennel (Crithmum maritimum). Plant Soil 1–12. https://doi.org/10.1007/s11104-021-04994-x.

Mozaffarian, D., Fahimi, S., Singh, G.M., Micha, R., Khatibzadeh, S., Engell, R.E., Lim, S., Danaei, G., Ezzati, M., Powles, J., 2014. Global sodium consumption and death from cardiovascular causes. N. Engl. J. Med. 371 (7), 624–634. https://doi.org/10.1056/NEJMoa1304127.

Nabet, N., Boudries, H., Chougui, N., Loupassaki, S., Souagui, S., Burló, F., Hernández, F., Carbonell-Barrachina, A.A., Madani, K., Larbat, R., 2017. Biological activities and secondary compound composition from Crithmum maritimum aerial parts. Int. J. Food Prop. 20 (8), 1843–1855. https://doi.org/10.1080/10942912.2016.1222541.

Nunes-Nesi, A., Fernie, A.R., Stitt, M., 2010. Metabolic and signaling aspects underpinning the regulation of plant carbon nitrogen interactions. Mol. Plant 3 (6), 973–996. https://doi.org/10.1093/mp/ssq049.

Ondrasek, G., Rengel, Z., 2021. Environmental salinization processes: detection, implications & solutions. Sci. Total Environ. 754, 142432. https://doi.org/10.1016/j.scitotenv.2020.142432.

Özcan, M., Pedro, L.G., Figueiredo, A.C., Barroso, J.G., 2006. Constituents of the essential oil of sea fennel (Crithmum maritimum L.) growing wild in Turkey. J. Med. Food 9, 128–130. https://doi.org/10.1089/jmf.2006.9.128.

Paul, M.J., Stitt, M., 1993. Effects of nitrogen and phosphorus deficiencies on levels of carbohydrates, respiratory enzymes and metabolites in seedlings of tobacco and their response to exogenous sucrose. Plant Cell Environ. 16 (9), 1047–1057. https://doi.org/10.1111/j.1365-3040.1996.tb02062.x.

Pavela, R., Maggi, F., Lupidi, G., Cianfaglione, K., Dauvergne, X., Bruno, M., Benelli, G., 2017. Efficacy of sea fennel (Crithmum maritimum L., Apiaceae) essential oils against Culex quinquefasciatus Say and Spodoptera littoralis (Boisd.). Ind. Crop. Prod. 109, 603–610. https://doi.org/10.1016/j.indcrop.2017.09.013.

R Core Team, 2021. R:A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria. https://www.R-project.org/.

Renna, M., 2018. Reviewing the prospects of sea fennel (Crithmum maritimum L.) as emerging vegetable crop. Plants 7 (4), 92. https://doi.org/10.3390/plants7040092.

Ryan, J., Rashid, A., Torrent, J., Yau, S.K., Ibrikci, H., Sommer, R., Erenoglu, E.B., 2013. Micronutrient constraints to crop production in the Middle East-West Asia region: significance, research, and management. Adv. Agron. 122, 1–84. https://doi.org/10.1016/B978-0-12-417187-9.00001-2.

Sánchez-Faure, A., Calvo, M.M., Pérez-Jiménez, J., Martín-Diana, A.B., Rico, D., Montero, M.P., Gómez-Guillén, M.C., López-Caballero, M.E., Martínez-Alvarez, O., 2020. Exploring the potential of common iceplant, seaside arrowgrass and sea fennel as edible halophytic plants. Food Res. Int. 137, 109613. https://doi.org/10.1016/j.foodres.2020.109613.

Schlüter, U., Mascher, M., Colmsee, C., Scholz, U., Bräutigam, A., Fahnenstich, H., Sonnewald, U., 2012. Maize source leaf adaptation to nitrogen deficiency affects not only nitrogen and carbon metabolism but also control of phosphate homeostasis. Plant Physiol. 160 (3), 1384–1406. https://doi.org/10.1104/pp.112.204420.

Schlüter, U., Colmsee, C., Scholz, U., Bräutigam, A., Weber, A.P., Zellerhoff, N., Bucher, M., Fahnenstich, H., Sonnewald, U., 2013. Adaptation of maize source leaf metabolism to stress related disturbances in carbon, nitrogen and phosphorus balance. BMC Genom. 14 (1), 1–25. https://doi.org/10.1186/1471-2164-14-442.

Shaer, H.M., Attia-Ismail, S.A., 2015. Halophytic and salt tolerant feedstuffs in the Mediterranean basin and Arab region: an overview. Halophytic and Salt-tolerant Feedstuffs, Impacts on Nutrition, Physiology and Reproduction of Livestock. CRC Press, Boca Raton, pp. 21–36.

Simopoulos, A.P., 2011. Importance of the omega-6/omega-3 balance in health and disease: evolutionary aspects of diet. Healthy Agriculture, Healthy Nutrition, Healthy People. Karger Publishers, pp. 10–21.

Singer, S.D., Zou, J., Weselake, R.J., 2016. Abiotic factors influence plant storage lipid accumulation and composition. Plant Sci. 243, 1–9. https://doi.org/10.1016/j.plantsci.2015.11.003.

Sousa, G., Alves, M.I., Neves, M., Tecelão, C., Ferreira-Dias, S., 2022. Enrichment of sunflower oil with ultrasound-assisted extracted bioactive compounds from Crithmum maritimum L. Foods 11 (3), 439. https://doi.org/10.3390/foods11030439.

Stahl, R.S., James, B.R., 1991. Zinc sorption by B horizon soils as a function of pH. Soil Sci. Soc. Am. J. 55 (6), 1592–1597. https://doi.org/10.2136/sssaj1991.03615995005500060015x.

Stepniewski, W., Glinski, J., Ball, B.C., 1994. Effects of compaction on soil aeration properties. In: Soane, B.D., van Ouwekerk, C. (Eds.), Soil Compaction in Crop Production. Elsevier, Netherlands, pp. 167–189.

Stewart, A.J., Chapman, W., Jenkins, G.I., Graham, I., Martin, T., Crozier, A., 2001. The effect of nitrogen and phosphorus deficiency on flavonol accumulation in plant tissues. Plant Cell Environ. 24 (11), 1189–1197. https://doi.org/10.1046/j.1365-3040.2001.00768.x.

Sun, X., Chen, J., Liu, L., Rosanoff, A., Xiong, X., Zhang, Y., Pei, T., 2018. Effects of magnesium fertilizer on the forage crude protein content depend upon available soil nitrogen. J. Agric. Food Chem. 66 (8), 1743–1750. https://doi.org/10.1021/acs.jafc.7b04028.

Suresh, U., Murugan, K., Panneerselvam, C., Cianfaglione, K., Wang, L., Maggi, F., 2020. Encapsulation of sea fennel (Crithmum maritimum) essential oil in nanoemulsion and SiO2 nanoparticles for treatment of the crop pest Spodoptera litura and the dengue vector Aedes aegypti. Ind. Crop. Prod. 158, 113033. https://doi.org/10.1016/j.indcrop.2020.113033.

Tsoukatou, M., Tsitsimpikou, C., Vagias, C., Roussis, V., 2001. Chemical intra-Mediterranean variation and insecticidal activity of Crithmum maritimum. Z. Naturforsch. C 56 (3–4), 211–215. https://doi.org/10.1515/znc-2001-3-407.

Ulbricht, T.L.V., Southgate, D.A.T., 1991. Coronary heart disease: seven dietary factors. Lancet 338 (8773), 985–992. https://doi.org/10.1016/0140-6736(91)91846-M.

Wacal, C., Ogata, N., Basalirwa, D., Sasagawa, D., Kato, M., Handa, T., Masunaga, T., Yamamoto, S., Nishihara, E., 2019. Fatty acid composition of sesame (Sesamum indicum L.) seeds in relation to yield and soil chemical properties on continuously monocropped upland fields converted from paddy fields. Agronomy 9 (12), 801. https://doi.org/10.3390/agronomy9120801.

Wilson, D.O., Boswell, F.C., Ohki, K., Parker, M.B., Shuman, L.M., Jellum, M.D., 1982. Changes in Soybean Seed Oil and Protein as Influenced by Manganese Nutrition 1. Crop Sci. 22 (5), 948–952. https://doi.org/10.2135/cropsci1982.0011183X002200050012x.

Wright, I.J., Reich, P.B., Westoby, M., Ackerly, D.D., Baruch, Z., Bongers, F., Cavender-Bares, J., Chapin, T., Cornelissen, J.H.C., Diemer, M., Flexas, J., Garnier, E., Groom, P.K., Gulias, J., Hikosaka, K., Lamont, B.B., Lee, T., Lee, W., Lusk, C., Midgley, J.J., Navas, M.L., Niinemets, U., Oleksyn, J., Osada, N., Poorter, H., Poot, P., Prior, L., Pyankov, V.I., Roumet, C., Thomas, S.C., Tjoelker, M.G., Veneklaas, E.J., Villar, R., 2004. The worldwide leaf economics spectrum. Nature 428 (6985), 821–827. https://doi.org/10.1038/nature02403.

Yeoh, H.H., Wee, Y.C., 1994. Leaf protein contents and nitrogen-to-protein conversion factors for 90 plant species. Food Chem. 49 (3), 245–250. https://doi.org/10.1016/0308-8146(94)90167-8.

Zenobi, S., Fiorentini, M., Ledda, L., Deligios, P., Aquilanti, L., Orsini, R., 2022. Crithmum maritimum L. biomass production in mediterranean environment. Agronomy 12 (4), 926. https://doi.org/10.3390/agronomy12040926.

Zobayed, S.M.A., Afreen, F., Kozai, T., 2007. Phytochemical and physiological changes in the leaves of St. John's wort plants under a water stress condition. Environ. Exp. Bot. 59 (2), 109–116. https://doi.org/10.1016/j.envexpbot.2005.10.002.