Carbon Stocks in Vegetation and Soil and Their Relationship with Plant Community Traits in a Mediterranean Non-tidal Salt Marsh

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Abstract

Salt marshes are considered among the ecosystems with the highest capacity for carbon sequestration. However, studies have mainly focused on tidal salt marshes, while knowledge about non-tidal salt marshes, which prevail in the Mediterranean Basin, is currently scarce. Consequently, we aimed to (1) estimate the carbon stocks of the vegetation, litter, and soil of three natural Habitats of Community Interest of a Mediterranean non-tidal salt marsh–a halophilous scrub, a salt meadow, and a glasswort sward–and (2) determine how differences in floristic composition and community structure among habitats over 1 year are related to the amount and distribution of carbon stored in plants and soils. Results show that the halophilous scrub and the salt meadow were constituted by mature plant communities with overall stable carbon stocks in the vegetation, litter, and soil (0–20 cm), which were approximately 4 and 2.5 times larger, respectively, than those found in the glasswort sward (1013 ± 40 g C m^{-2}). However, while the salt meadow and the glasswort sward had more carbon stored in the soil than in the vegetation (approximately 3 and 7.5 times more, respectively), the halophilous scrub had similar amounts in both compartments (2248 ± 388 and 1566 ± 179 g C m^{-2} in the soil and vegetation, respectively). *Sarcocornia fruticosa* represented 93.5% of the total plant biomass of the halophilous scrub, which highlights the importance of this species in maintaining carbon stocks in this Mediterranean non-tidal salt marsh.

Keywords Blue carbon · Coastal wetlands · Habitats of Community Interest · Halophytes · Plant biomass · Salt marsh plant communities

Introduction

Salt marshes are among the ecosystems with the highest carbon sequestration capacity (McLeod et al. 2011), mainly due to high rates of primary production (Mitsch and Gosselink 2015) and low rates of soil organic matter decomposition, promoting carbon accumulation in the soil (Chmura et al.

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2003). However, there are still important knowledge gaps in the carbon storage function of these ecosystems. In this sense, studies of net primary production and/or standing biomass have been broadly performed in tidal salt marshes, especially in North America (de la Cruz 1974; Linthurst and Reimold 1978; White et al. 1978; Hopkinson et al. 1980; Connor 1995; Darby and Turner 2008), and even in Europe (Benito and Onaindia 1991; Bouchard et al. 1998; Bouchard and Lefeuvre 2000; Figueroa et al. 2003; Neves et al. 2010; Castillo et al. 2021), while literature on coastal non-tidal salt marshes is scarce (Berger et al. 1978; Ibañez et al. 1999; Curcó et al. 2002; Scarton et al. 2002). Non-tidal salt marshes prevail in the Mediterranean Basin due to the low tidal range of the Mediterranean Sea (0.1–1 m compared to 1–10 m in tidal salt marshes; Ibañez et al. 2000). The absence of daily tides combined with low rainfall and high summer temperatures causes prolonged conditions of soil aridity and hypersalinity, which limits plant growth and affects carbon sequestration capacity of vegetation (Ibañez et al. 2000; Curcó et al. 2002). Furthermore,

most of the studies analysing plant primary production in salt marshes have focused on aboveground organs, despite belowground organ production sometimes being much higher (Chmura 2011). Indeed, while roots remain in the soil ready to be decomposed in situ, aboveground biomass is susceptible to being exported outside the salt marsh. In the Mediterranean Basin salt marshes, despite the importance of the root system in vegetation and soil carbon storage, only in few studies have measured its biomass (Curcó et al. 2002; Scarton et al. 2002).

In salt marshes, soils also play a very important role in carbon storage capacity, with the amount of carbon stored in soils usually higher than in vegetation (Dalal and Allen 2008). In tidal salt marshes, long periods of flooding can create anoxic conditions, reducing the efficiency of organic matter decomposition and favouring soil carbon sequestration (Megonigal et al. 2004). Consequently, tidal salt marshes are among the ecosystems with the highest soil carbon sequestration capacity (Duarte et al. 2005). However, carbon stored in soils of Mediterranean non-tidal salt marshes has been much less studied. In fact, of the 96 studies reviewed by Chmura et al. in 2003, only one included data from the Mediterranean Basin (Hensel et al. 1999). Since then, just a few more studies have been performed in Mediterranean Basin salt marshes, reporting similar values to those obtained for temperate tidal salt marshes (Curcó et al. 2002; Scarton et al. 2002). However, considering the high spatial variability of this type of salt marsh (Ibañez et al. 2000), more studies are needed to confirm these results.

Carbon stocks in salt marshes also depend on the floristic composition and community structure (Elsey-Quirk et al. 2011; Ford et al. 2019). On the one hand, species composition and diversity of plant communities can largely determine the amount of above- and belowground plant biomass, as well as litter production and decomposition (Ford et al. 2016). On the other hand, the stage of maturity of a plant community can also affect its carbon sequestration capacity, since more mature stands usually have lower vegetation growth (Yu et al. 2017). Despite this, few studies have investigated these relationships (Elsey-Quirk et al. 2011; Ford et al. 2019) and, as far as we know, none of them in Mediterranean non-tidal salt marshes.

La Pletera is a typical non-tidal Mediterranean salt marsh composed of different Habitats of Community Interest (HCIs), which have been defined by the European Union's Habitats Directive (Council Directive 92/43/EEC, see Annex 1 of the Directive, European Commision, 1997) as those habitats with a high ecological value that are in danger of disappearance and whose natural range mainly falls within the territory of the European Union. The main HCIs found at La Pletera are halophilous scrubs (HCI code 1420) and salt meadows (HCI code 1410) dominated by perennial species, and glasswort swards (HCI code 1310) dominated by annual

species. Considering the interest of these habitats and the knowledge gaps identified above, the main aims of this study were (1) to estimate the vegetation (above and belowground) and soil carbon stocks of these three natural habitats at La Pletera salt marsh and (2) to determine whether differences in floristic composition and community structure among habitats over 1 year are related to the amount and distribution of carbon stored in plants and soils. We hypothesized that (1) the habitat with the highest plant cover and dominated by perennial and woody species would show a higher amount of carbon stored in the vegetation and soil, and less changes over a year; and (2) in the three habitats, soil would have a higher amount of stored carbon than vegetation. The information provided by this study can help in the management and revaluation of these coastal salt marshes, which have traditionally been subjected to a high urban pressure (Airoldi and Beck 2007) and might contribute to promote their conservation, and restoration in the case of degraded areas.

Materials and Methods

Study Area

The study was performed at La Pletera, a coastal Mediterranean non-tidal salt marsh located in the north of the river Ter mouth in the municipality of Torroella de Montgrí (Girona, NE of the Iberian Peninsula, 42°1′51″N 3°11′33″E, Fig. 1). La Pletera salt marsh presents a coastal Mediterranean climate with the lowest temperatures found in winter and the highest in summer (Fig. S1). The seasons with the highest monthly accumulated rainfall are usually autumn and spring. Total accumulated rainfall for the years 2015 and 2016, when the study was conducted, was 316.6 and 487.4 mm year^{-1}, respectively. Astronomical tides are almost imperceptible (generally 0.2–0.3 m), being meteorological events, like strong easterly winds and rainfall, the main cause of flooding, either by direct water input from the sea or by the rainfall itself and the concomitant rise of the aquifer water table (Menció et al. 2017). The largest floods happen when rainfall and sea storms occur at the same time, which mostly takes place in autumn (Pascual and Martinoy 2018).

Floristic Composition and Community Structure

The study of the vegetation composition and community structure of the three habitats was performed by means of the point quadrat method (Heslehurst 1971), using a grid frame of 80 × 80 cm with 64 points separated 10 cm. A vertical metal pin with a diameter of 7 mm was used to record, for each point of the grid, the maximum height of each plant species touching the pin, distinguishing the following parts: living green biomass, living woody biomass, and standing
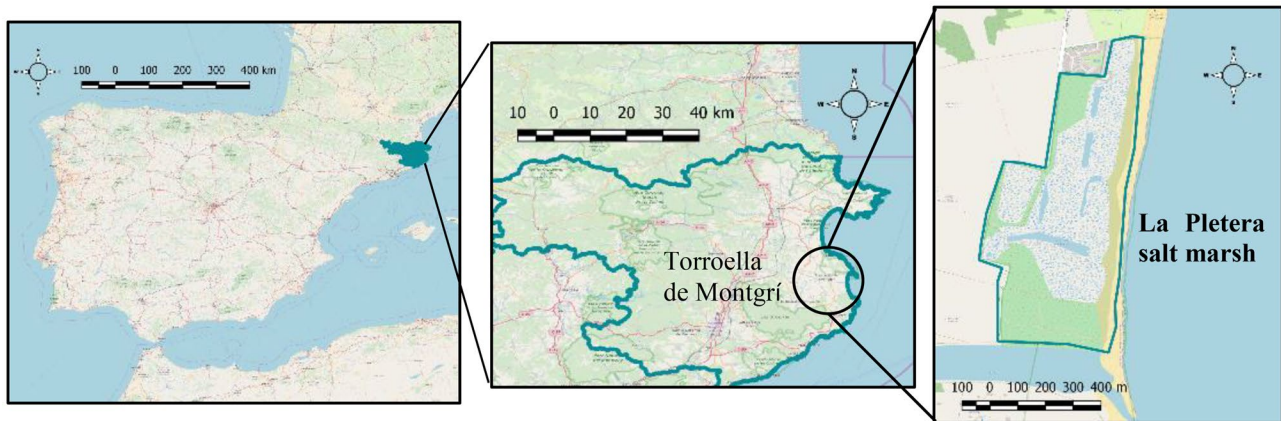
Fig. 1 Geographical location of La Pletera salt marsh. On the left, Girona province (NE of the Iberian Peninsula); at the centre, Torroella de Montgrí municipality; on the right, La Pletera salt marsh

dead tissues. Five randomly selected plots (80 × 80 cm) per habitat were sampled in summer 2015 and 2016 (Fig. S2).

For each plot, the following parameters were calculated: percentage of plant cover, percentage of living plant cover, species richness (*S*), relative abundance of the dominant species (*p*$_i$), Shannon-Wiener index of biodiversity (*H*), maximum height of the vegetation, and maximum height of the living parts of the vegetation. *H* was determined using the following equation: $H = -\sum_{i=1}^{S} p_i \, log_2 p_i$, where p_i is the relative abundance of the species and *S* is the species richness.

Plant Biomass and Carbon Storage

In summer 2015 and 2016, we harvested all the aboveground plant biomass from the same randomly selected plots used for floristic composition (Fig. S2). After removing the aerial plant biomass, superficial litter (leaves and stems) was collected in a quarter of each one of the plots, and plant roots were sampled at 0–20 cm by the extraction of three soil cores (8-cm diameter, 20-cm long; Eijkelkamp auger set, Netherlands) per plot. Root sampling was performed at 0–20 cm because previous sampling demonstrated that 83, 75, and 94% of the belowground biomass of the halophilous scrub, the salt meadow, and the glasswort sward, respectively, was located at this depth.

Once in the laboratory, aboveground plant biomass from each plot and habitat was sorted by species and then by living green, living woody, and standing dead biomass. Roots were also separated from soil samples by sieving and then litter and roots were rinsed with tap water to eliminate residual soil particles. All the plant material was dried in an oven at 70 °C to constant weight.

For the dominant species of each habitat, dried plant material of each aboveground fraction was homogenized with a grinder (Taurus, Spain) to estimate the amount of carbon

stored in each fraction. In the case of the salt meadow, biomass and carbon content of the non-dominant species were also determined since they represented a considerable percentage of the total biomass. Roots and litter collected in the plots were mixed and homogenized. The amount of dried plant material homogenized was 25–50%, 50–70%, and 100% of total when the total weight of the fraction was higher than 80 g, 15–80 g, or lower than 15 g, respectively.

To estimate the carbon content per dry weight of each fraction, a part of the homogenized material (two vials of 2 ml capacity) was ground to fine powder with a ball mill (Mixer Mill MM 400, Retsch GmbH, Germany), and then two subsamples of 4 mg per plot were weighted (microbalance Sartorius 2MP, Germany) and placed in tin capsules. Carbon analysis was performed using a PDZ Europa ANCA-GSL elemental analyser interfaced to a PDZ Europa 20–20 isotope ratio mass spectrometer (Sercon Ltd., UK) at the Stable Isotope Facility of the University of California (Davis, USA). For each plot, carbon stored in the vegetation (g C m^{-2}) was estimated by multiplying the carbon content (mg C g DW^{-1}) of each plant fraction by its total dry weight (g DW m^{-2}), considering only the dominant species in the halophilous scrub and the glasswort sward (which represented above the 95% of the total biomass) and all the species in the case of the salt meadow.

Soil Characteristics and Organic Carbon Storage

For each one of the five plots where plant biomass was harvested per habitat, one composite soil sample was obtained at 0–20-cm depth in summer 2015 and 2016 by mixing the three soil cores extracted for plant belowground biomass sampling, after separating the roots from the soil. As for the roots, only the first 20 cm were sampled, since previous sampling showed that most of the soil carbon was located at

the first 20 cm (72, 70, and 65% for the halophilous scrub, salt meadow, and glasswort sward, respectively).

To characterise the soil of the three habitats, the following physical and biochemical parameters were analysed: pH, electrical conductivity (EC), textural classes, bulk density (BD), soil organic carbon (SOC), and total nitrogen (TN). Before the analyses, samples were air-dried and sieved to 2 mm. Soil pH was determined potentiometrically in distilled water and with a soil:water ratio 1:2.5 using a Crison 20 pH meter (Crison Instruments, Spain). Electrical conductivity was measured with a soil:water ratio 1:5 using a Crison micro CM 2200 conductivity meter (Crison Instruments, Spain). Soil textural classes were determined following the method described in Porta et al. (1994). Concretely, the percentage of sand was determined using sieves with different mesh sizes (200 and 20 μm), whereas the percentage of silt and clay were estimated using a calibrated volumetric pipette and considering the principle of sedimentation of soil particles. The dimensional classes estimated were 2000–20 μm for sand fraction, 20–2 μm for silt, and < 2 μm for clay fraction according to the International Society of Soil Science (ISSS). Soil BD was estimated by collecting an extra sample with a known volume of soil at each plot and weighting it after being dried at 105 °C to constant weight. SOC (%) was quantified by the dichromate wet oxidation method (Walkley and Black 1934) in the presence of concentrated sulphuric acid, while TN was estimated by means of the Kjeldahl method (Van Reeuwijk 2002). Electrical conductivity, pH, and TN were estimated in three composite soil samples per habitat in 2015 and in five composite soil samples per habitat in 2016. Soil textural classes were determined in the five samples per habitat of 2016, while SOC (%) and BD were analysed in the five plots studied each year (2015 and 2016). The amount of organic carbon stored at 0–20 cm, expressed in g C m^{-2}, was estimated from SOC and BD values.

Data Analyses

To evaluate our first hypothesis, we performed two-way ANOVAs (with habitat and year, or with species and year for each habitat, as fixed factors) using as variables the studied parameters related with the floristic composition and structure of the community as well as the amount of carbon stored in the different fractions of the vegetation and soil. For the aboveground plant fractions (living green, living woody, and standing dead biomass), two-way ANOVAs were performed considering each fraction separately. To determine whether there were significant differences in the carbon stored among plant fractions for each one of the most abundant species of each habitat, two-way ANOVAs were also used (with year and fraction as fixed factors). To check our second hypothesis, we analysed, for each habitat, the differences in the

amount of carbon stored in the soil and vegetation (above and belowground) using one-way ANOVAs.

In the two-way ANOVAs, whenever the interaction between the two factors was significant, differences between years (for each habitat or species) and among habitats, species, or fractions (within each year) were evaluated by means of one-way ANOVAs. Conversely, when the interaction and the factor year were not significant, one-way ANOVAs were performed pooling the data for the two years.

The Shapiro-Wilk test was used to test normality, while the homogeneity of variances was analysed with the Levene's test. Tukey's HSD post hoc tests were applied when there were significant differences among habitats, species, or fractions. When the assumptions of normality and/or homoscedasticity were not reached, even after transforming the data, the non-parametric Mann-Whitney or Kruskal-Wallis tests were applied, followed by pairwise comparisons when the factor had a significant effect. For all the statistical tests, the significance level considered was p value < 0.05. Statistical analyses were done using SPSS software (IBM SPSS statistics, USA).

Results

Floristic Composition and Community Structure

In each habitat, the number of species identified varied between 7 and 15 (Table S1), with one or two dominant species having a relative abundance above 60% (Table 1). The most abundant species of the halophilous scrub was *Sarcocornia fruticosa* (L.) A. J. Scott (syn. *Arthrocnemum fruticosum* (L.) Moq.). In the glasswort sward, *Salicornia patula* Duval-Jouve was the most abundant species, but in 2016 *S. fruticosa* appeared with a relative abundance of approximately 21%. *Elytrigia atherica* (Link) Kerguélen (syn. *Elymus pycnanthus* (Godr.) Melderis), and *Halimione portulacoides* (L.) Aellen (syn. *Atriplex portulacoides* L.) were the dominant species of the salt meadow.

Sarcocornia fruticosa and *H. portulacoides* are shrub species from the Chenopodiaceae family. *Sarcocornia fruticosa* has highly reduced leaves and succulent photosynthetic green stems, while *H. portulacoides* is a creeping subshrub with slightly fleshy leaves. *Salicornia patula* (Chenopodiaceae) is an annual succulent herb with, similarly to *S. fruticosa*, highly reduced leaves and succulent photosynthetic stems, while *E. atherica* (Poaceae) is a perennial herbaceous species.

Relative abundance of the dominant species did not change over the studied year in any of the three habitats (Table 1), and neither did the studied parameters related to plant community structure for the halophilous scrub and the salt meadow. In contrast, for the glasswort sward, the maximum height of the vegetation doubled or tripled

Table 1 Relative abundance (mean ± SE, $n = 5$) of the most abundant species of each habitat (HCI: Habitat of Community Interest) in July 2015 and July 2016

HCI	Species	Year	Relative abundance (%)	p value
Halophilous scrub	*Sarcocornia fruticosa*	2015	75.0 ± 13.5	0.768
		2016	69.3 ± 12.9	
	Halimione portulacoides	2015	2.9 ± 1.3	0.841
		2016	12.4 ± 8.8	
Salt meadow	*Elytrigia atherica*	2015	60.4 ± 8.5	0.981
		2016	60.7 ± 10.0	
	Halimione portulacoides	2015	20.5 ± 7.0	0.947
		2016	19.7 ± 9.0	
Glasswort sward	*Salicornia patula*	2015	98.4 ± 1.2	0.095
		2016	73.2 ± 18.6	
	Suaeda maritima	2015	1.6 ± 1.2	0.690
		2016	5.2 ± 3.4	
	Sarcocornia fruticosa	2015	0 ± 0	-
		2016	20.6 ± 19.9	

The effect of the sampling year (*p* value) is given

(depending on the parameter) from one year to the next ($p < 0.001$, $n = 5$; Table 2). The halophilous scrub and the salt meadow showed almost complete or complete plant cover, while in the glasswort sward plant cover was about 80% ($p < 0.001$, $n = 10$; Table 2). The salt meadow had the highest plant species richness and diversity, although differences with the halophilous scrub were not significant. The Shannon-Wiener index was always below 2 for the three habitats, indicating low plant species diversity, especially in the case of the glasswort sward (Table 2).

Plant Biomass and Carbon Storage

No significant differences in living, dead, and total aboveground plant biomass, belowground plant biomass, or litter biomass were found between 2015 and 2016 for any of the three habitats (Fig. 2). The halophilous scrub was by far the habitat with the highest total and living aboveground biomass which were about 76% and 90% higher than in the salt meadow and the glasswort sward, respectively ($p < 0.001$, $n = 10$; Fig. 2a, b). Meanwhile, for the halophilous scrub and the salt meadow, the standing dead biomass and the belowground plant biomass were similar, about 83% and 80% higher than that of the glasswort sward, respectively ($p < 0.001$, $n = 10$; Fig. 2c, d). The halophilous scrub and the salt meadow also presented 94% and 92% higher litter amount than the glasswort sward, respectively ($p < 0.001$, $n = 10$; Fig. 2e).

Carbon content (µg C mg DW^{-1}) of living aboveground plant fractions of the most abundant species of each habitat

Table 2 Parameters related to plant community structure (mean ± SE, $n = 5$) of the three habitats of La Pletera salt marsh

HCI	Year	Plant cover (%)	Living plant cover (%)	Maximum height of vegetation (cm)	Maximum height of living vegetation (cm)	Species richness	Shannon-Wiener Index
Halophilous scrub	2015	98.1 ± 1.5	87.2 ± 7.6	49.5 ± 6.6	46.7 ± 5.5	2.8 ± 0.6	0.73 ± 0.33
	2016	99.4 ± 0.6 a	92.2 ± 7.4 a	46.8 ± 7.2 a	46.0 ± 7.0 a	2.4 ± 0.7 ab	0.79 ± 0.34 ab
Salt meadow	2015	100.0 ± 0.0	93.1 ± 3.7	42.5 ± 5.6	40.1 ± 5.2	3.4 ± 0.5	1.29 ± 0.21
	2016	100.0 ± 0.0 a	99.4 ± 0.4 a	43.7 ± 4.0 a	41.2 ± 4.1 a	4.2 ± 0.9 a	1.28 ± 0.27 a
Glasswort sward	2015	79.7 ± 3.7	66.3 ± 5.9	**5.8 ± 0.5 ***	**3.6 ± 0.5 ***	1.4 ± 0.3	0.09 ± 0.06
	2016	78.4 ± 5.7 b	49.4 ± 11.5 b	**10.6 ± 1.6 *** b	**9.8 ± 1.2 *** b	1.8 ± 0.4 b	0.31 ± 0.16 b

Different letters indicate significant differences among habitats, considering, for each habitat, all the data of both years jointly. Values marked in bold and with asterisks indicate significant differences between years within each habitat

HCI Habitat of Community Interest

did not vary significantly between years (Fig. 3a, b). *Elytrigia atherica* had the highest carbon content in green tissues, while *S. patula* had the lowest (almost 40% lower than *E. atherica*; *p* < 0.001, *n* = 10; Fig. 3a). Regarding the carbon content of the woody fraction, *S. fruticosa* from the halophilous scrub showed similar values to those of *H. portulacoides* from the salt meadow, but it was about 11% higher than that of *S. fruticosa* from the glasswort sward (*p* = 0.006, *n* = 10; Fig. 3b). Differences between years were observed in the carbon content of the standing dead fraction of *E. atherica* and *S. patula*, which was approximately 3% and 12% higher in 2016 than 2015, respectively (*p* = 0.002 and 0.044, respectively, *n* = 5; Fig. 3c). Among species, *S. patula* showed the lowest carbon content in the standing dead fraction in 2015, while in 2016 values did not differ from those of *H. portulacoides* (*p* < 0.001, *n* = 5; Fig. 3c). In the glasswort sward, *S. fruticosa* presented standing dead tissues in only one plot in 2016, with a carbon content of 449.5 µg C mg DW^{-1}.

Carbon content of the belowground plant biomass was 8%, 5%, and 6% lower in 2016 than in 2015 for the halophilous scrub, the salt meadow, and the glasswort sward, respectively (*p* = 0.006, *n* = 5; Fig. 4a). Irrespective of the year, the habitat with the highest carbon content in the belowground plant fraction was the salt meadow, with values 8% and 14% higher than the halophilous scrub and the glasswort sward, respectively (*p* < 0.001, *n* = 10; Fig. 4a). Regarding litter C content, it was 5% and 24% higher in 2016 than in 2015 in the halophilous scrub and the glasswort sward, respectively (*p* = 0.004 and 0.011, respectively, *n* = 5; Fig. 4b). Irrespective of the year, the litter carbon content in the glasswort sward was 26% and 25% lower than in the halophilous scrub and the salt meadow, respectively (*p* < 0.001, *n* = 10; Fig. 4b).

The estimated carbon stocks (g C m^{-2}) of the plant fractions and litter did not differ between years for any of the studied habitats. In accordance with our first hypothesis, the halophilous scrub, dominated by perennial woody species, had approximately 3- and 15-fold higher carbon stored in the aboveground plant biomass (living plus standing dead) than the salt meadow and glasswort sward, respectively (*p* < 0.001, *n* = 10; Fig. 5, Table S2). Furthermore, the halophilous scrub and the salt meadow had more carbon in the belowground plant fraction (0–20-cm depth) and litter than the glasswort sward, dominated by annual species (*p* < 0.001, *n* = 10; Fig. 5, Table S2).
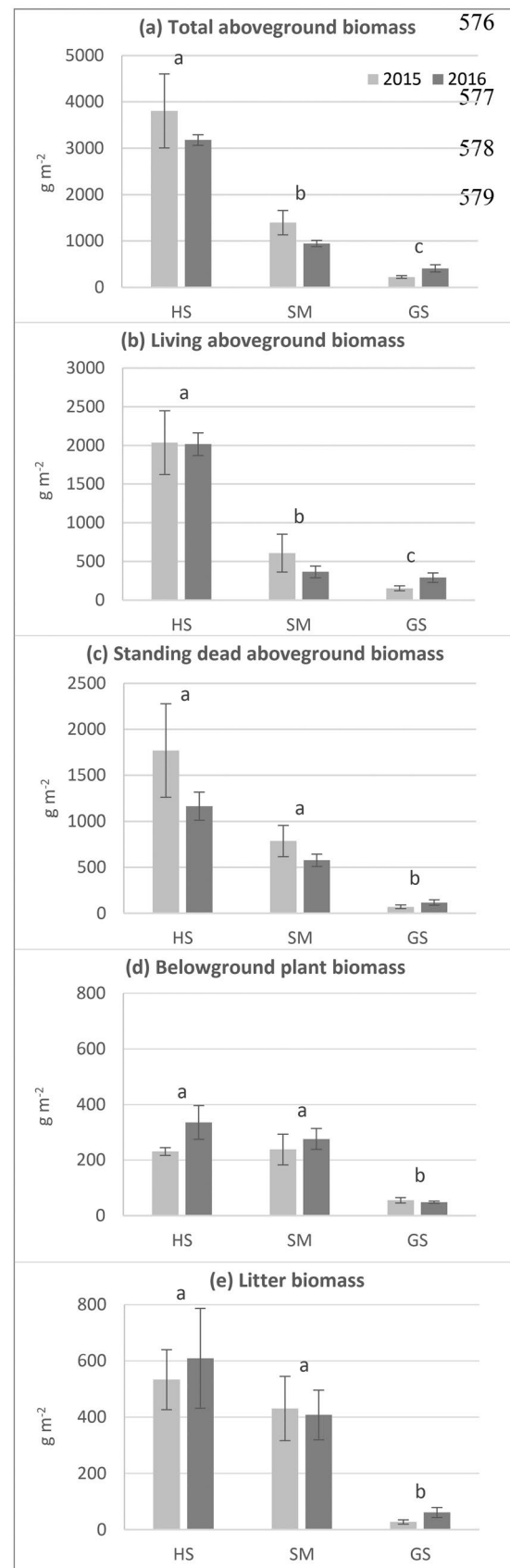
Fig. 2 Aboveground plant biomass (**a**, total; **b**, living; **c**, standing dead), root biomass at 0–20-cm depth (**d**), and litter biomass on the soil surface (**e**) of the three habitats in 2015 and 2016. HS, halophilous scrub; SM, salt meadow; GS, glasswort sward. Error bars represent the standard error of the mean (*n* = 5). Different letters indicate significant differences among habitats

Fig. 3 Carbon content per dry weight in aboveground plant fractions (**a**, living green; **b**, living woody; **c**, standing dead) of the most abundant species of each habitat. HS, halophilous scrub; SM, salt meadow; GS, glasswort sward. Error bars represent the standard error of the mean ($n = 5$). Values of *S. fruticosa* of the glasswort sward correspond only to 2016, since this species was not present in 2015. Asterisks indicate significant differences between years for each species. Different letters indicate significant differences among habitats or species considering $n = 10$ in panels a and b, since no differences between years were significant, and $n = 5$ in panel c, where lowercase and capital letters indicate significant differences among species for 2015 and 2016, respectively
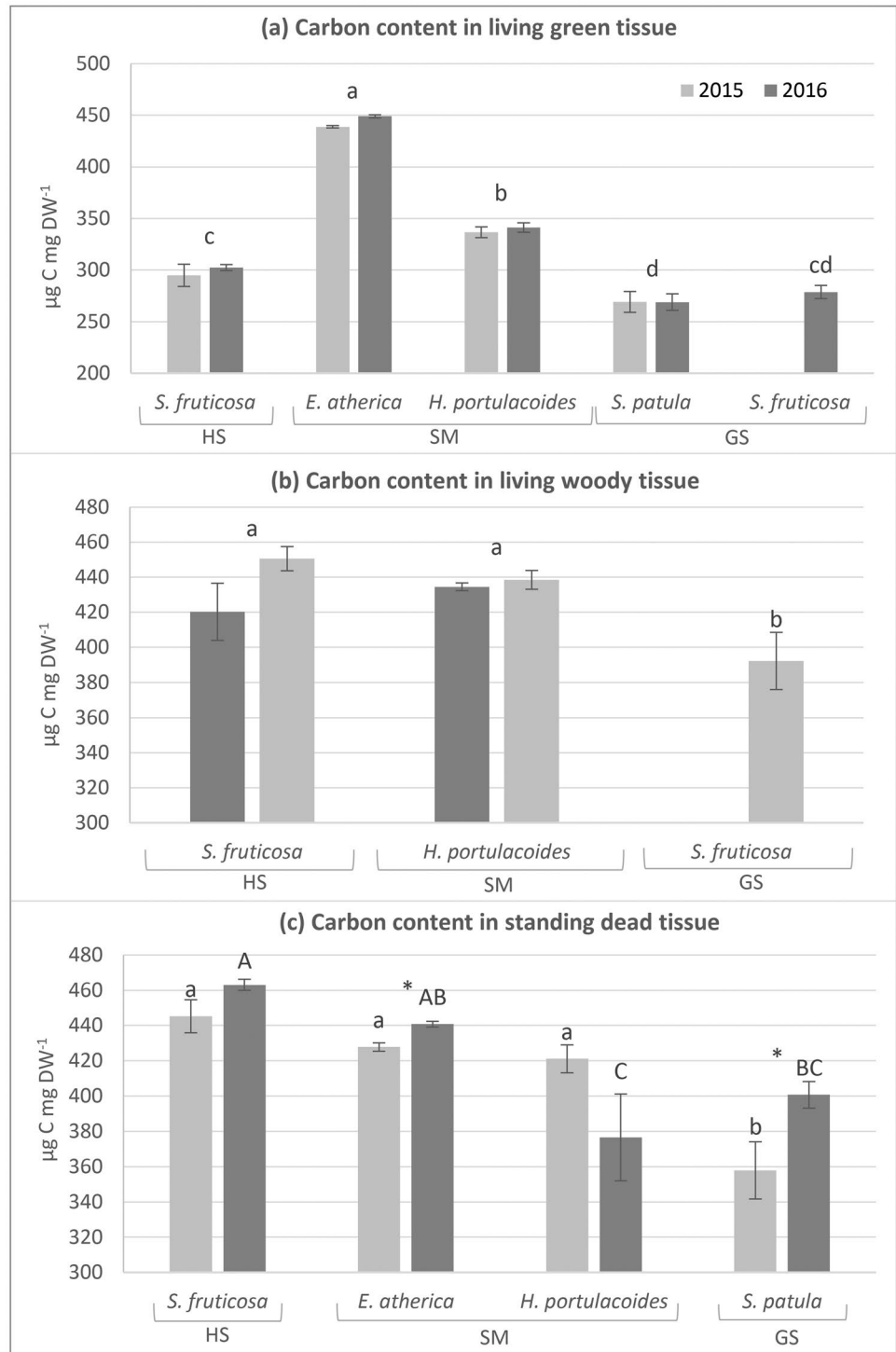
At the species level, *S. fruticosa*, which accounted for ≈ 94% of the total plant biomass of the halophilous scrub (Table S3), had between 5 and 6 times more carbon in the living woody and standing dead biomass than in the living green tissue ($p < 0.001$, $n = 10$; Table 3). In the same line, *E. atherica*, which represented ≈ 68% of the total plant biomass of the salt meadow (Table S3), had between 3 and 4 times more carbon in the standing dead fraction (it is an herbaceous species) than in the living green tissue ($p < 0.001$, $n = 10$; Table 3). Last, in *S. patula*, which accounted for ≈ 99% and 72% of the total plant biomass of the glasswort sward in 2015 and 2016, respectively (Table S3), the amount of carbon in its living and dead tissues was similar (Table 3).
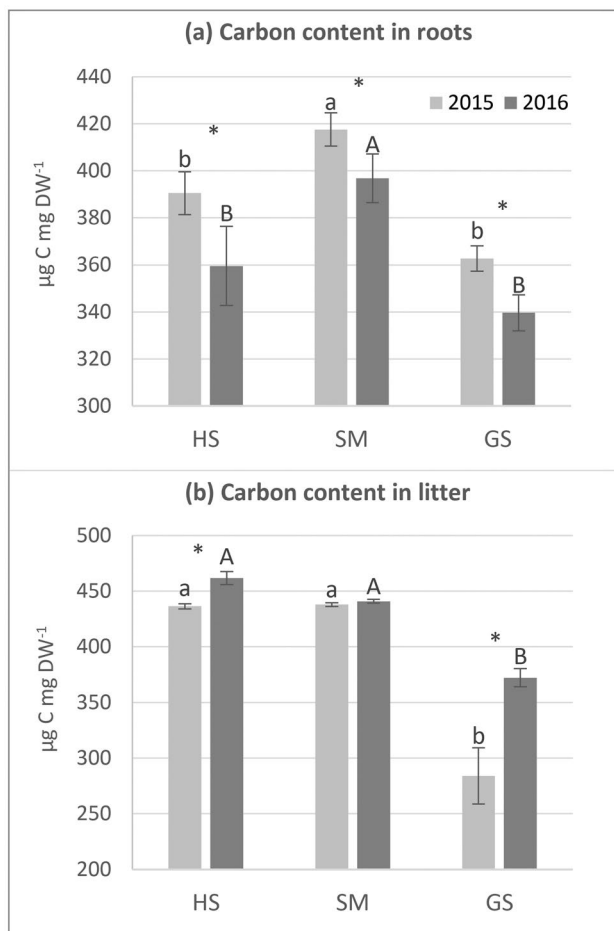
Fig. 4 Carbon content per dry weight in the belowground plant fraction (**a**) and in the litter (**b**) of the three habitats. HS, halophilous scrub; SM, salt meadow; GS, glasswort sward. Error bars represent the standard error of the mean ($n = 5$). Asterisks indicate significant differences between years for each habitat. Different lowercase and capital letters indicate significant differences among habitats for 2015 and 2016, respectively

Soil Characteristics and Organic Carbon Storage

Soils of the three habitats were slightly alkaline, with the glasswort sward showing higher soil pH than the halophilous scrub ($p = 0.001$, $n = 8$; Table 4). The halophilous scrub and the glasswort sward had soil electrical conductivity values of 5.6 ± 0.8 dS m^{-1} and 5.3 ± 0.8 dS m^{-1} (approximately 3.0 ppt of salinity, Table S4), respectively, being both of them more saline than the salt meadow ($p < 0.001$, $n = 8$), which presented values of 1.3 ± 0.4 dS m^{-1} (approximately 0.6 ppt of salinity, Table S4). These values of soil electrical conductivity (and thus salinity) were in the lower part of the soil salinity range obtained in a parallel study conducted in these habitats where soil salinity was measured along 1 year. In this other study, soil salinity ranged from 0.17 to 29.04 ppt in the halophilous scrub, from 2.26 to 42.90 ppt

in the glasswort sward, and from 0.02 to 3.63 ppt in the salt meadow (unpublished data). The high fluctuation in the soil salinity of these habitats is related to sea water storms, rainfall events, and the level of the aquifer (Mencló et al. 2017). The proportions of sand, silt, and clay of these soils were also highly variable (Table 4), which could have masked possible differences among habitats in soil texture. Neither did soil bulk density differ among habitats. The halophilous scrub and the salt meadow had 62% and 56% higher SOC ($p < 0.001$, $n = 10$) and 49% and 50% higher TN ($p = 0.002$, n = 8) than the glasswort sward, respectively; consequently, the C/N ratio did not vary among habitats (Table 4).

The soil carbon stocks (g C m^{-2}) estimated at 0–20-cm depth did not differ between years for any of the studied habitats. The halophilous scrub and the salt meadow had higher soil carbon stocks than the glasswort sward ($p < 0.001$, $n = 10$; Fig. 5, Table S2). Regarding our second hypothesis, we found that carbon stocks of the soil (0–20 cm depth) and vegetation (above plus belowground at 0–20 cm depth) of the halophilous scrub were similar ($p = 0.199$, $n = 10$; Fig. 4, Table S2), while the other two habitats stored much more carbon in the soil than in the vegetation ($p < 0.001$ for both habitats, $n = 10$; Fig. 5, Table S2).

Discussion

Salt marshes are considered species-poor ecosystems, since high salinity and temporary flooding limit the establishment of sensitive plant species, allowing only the survival of highly specialized ones (Adam 1990). According to this, the three habitats studied at La Pletera, a coastal non-tidal Mediterranean salt marsh, presented low values of plant species richness and biodiversity. Two of these habitats, the halophilous scrub and the salt meadow, presented mature plant communities, with a plant cover above 98% and no changes in the plant community structure and composition over the study period. In line with our first hypothesis, these two habitats showed a higher amount of carbon stored in the vegetation, litter, and soil than the glasswort sward, giving support to the idea that a greater maturity of the plant community is related to higher carbon stocks (Yu et al. 2017). In particular, the halophilous scrub showed the highest amount of carbon stored in the aboveground vegetation due to the elevated biomass of the dominant perennial woody species, *S. fruticosa*, which represented $93.5 \pm 2.9\%$ of the total biomass of this habitat. This carbon is basically stored in the woody and standing dead fractions of plants. Hence, these results highlight the important role of *S. fruticosa* in the carbon storage of non-tidal salt marshes.

Comparing the results of our study with previous findings for non-tidal salt marshes of the Mediterranean Basin, the estimated aboveground biomass of the halophilous scrub
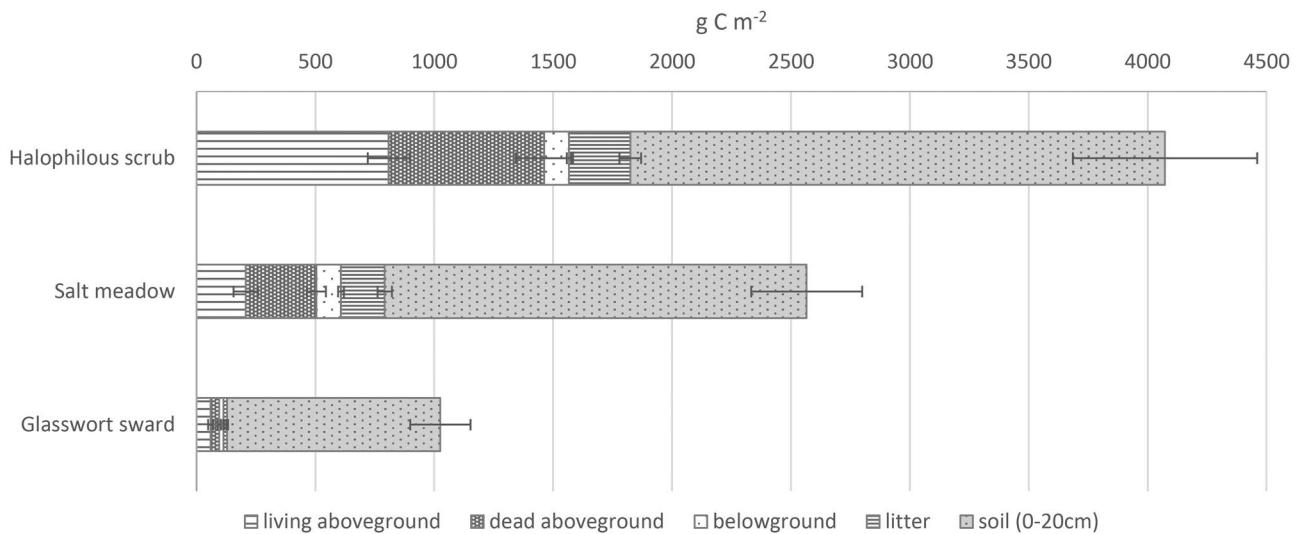
Fig. 5 Carbon stored in the vegetation (living and dead aboveground and belowground biomass), litter, and soil (0–20-cm depth) per square meter (g C m.$^{-2}$). Error bars represent $\pm$ standard errors of the mean ($n = 10$)

(mean value for the two years: 3492 $\pm$ 393 g m^{-2}) is in the upper part of the range obtained for salt marshes dominated by *S. fruticosa* (588 to 3515 g m^{-2}) (Curcó et al. 2002). In contrast, belowground plant biomass is much lower (283 $\pm$ 34 g m^{-2} at 0–20 cm depth) than in the Po (Scarton et al. 2002) and Ebro deltas (Curcó et al. 2002), where estimated values were 4200 g m^{-2} (at 0–30-cm depth) and 1050 g m^{-2} (at 0–20-cm depth), respectively. These results suggest that *S. fruticosa* plants growing at La Pletera might be experiencing more favourable environmental conditions than those from other Mediterranean non-tidal salt marshes, since a higher investment in belowground tissues compared to the aerial part is a typical response of halophytes to cope with stressful environmental conditions (Valentim et al. 2013).

Regarding the estimated aboveground biomass for the salt meadow and the glasswort sward (1171 $\pm$ 148 and 317 $\pm$ 49 g m^{-2}, respectively), values obtained were slightly lower than those reported for other salt marshes dominated by the same or similar species, although, in this case, only studies from tidal salt marshes were available. Indeed, studies in

tidal salt marshes of Cantabria (North Spain) (Benito and Onaindia 1991), Britain and Normandy (North France) (Bouchard and Lefeuvre 2000), Portugal (Caçador et al. 2004) and West Andalusia (South Spain) (Castillo et al. 2021) have reported values of total aboveground biomass of 1000–2500 g m^{-2} in areas dominated by *H. portulacoides*, 2600 g m^{-2} in areas dominated by *E. atherica*, and 480 and 550 g m^{-2} in areas dominated by *S. maritima* and *Salicornia ramosissima*, respectively (i.e., pioneer succulent annual vegetation). Despite plant belowground biomass at 0–20-cm depth for the salt meadow of La Pletera might be slightly underestimated (representing about 75% of the total root biomass), the estimated value was notably lower (257 $\pm$ 32 g m^{-2}) than the values reported for the entire root system of *E. atherica* and *H. portulacoides* ($\approx$ 4000 and 5800 g m^{-2}, respectively) in a tidal salt marsh of the Northeast Atlantic (The Netherlands) (Groenendijk and Vink-Lievaart 1987), and for *H. portulacoides* ($\approx$ 4300 g m^{-2}) in a tidal salt marsh in Southwest Spain (Castillo et al. 2021). Climate might contribute to explaining the differences observed between these

Table 3 Biomass and estimated carbon of each aboveground plant fraction (living green, living woody in the case of *Sarcocornia fruticosa*, and standing dead) for the most abundant species of each habitat (mean $\pm$ SE, $n = 10$)

	Plant fraction	Biomass (g C m^{-2})	Carbon (g C m^{-2})
Sarcocornia fruticosa (Halophilous scrub)	Living green	404.2 $\pm$ 59.8 a	120.1 $\pm$ 17.4 a
	Living woody	1512.4 $\pm$ 180.6 b	663.9 $\pm$ 78.1 b
	Standing dead	1423.8 $\pm$ 265.9 b	652.2 $\pm$ 121.0 b
Elytrigia atherica (Salt meadow)	Living green	174.2 $\pm$ 17.9 a	77.2 $\pm$ 7.8 a
	Standing dead	598.3 $\pm$ 105.5 b	260.0 $\pm$ 45.9 b
Salicornia patula (Glasswort sward)	Living green	186.5 $\pm$ 45.5 a	49.2 $\pm$ 11.4 a
	Standing dead	87.1 $\pm$ 16.5 a	33.2 $\pm$ 6.2 a

Different letters indicate significant differences among fractions within the same species

Table 4 Mean ± SE for the soil physical and biochemical parameters analysed (at 0–20-cm depth) in each habitat: pH, electrical conductivity (EC), sand, silt and clay proportions, bulk density (BD), soil organic carbon (SOC), total nitrogen (TN), and C/N ratio ($n = 10$ for SOC and BD; $n = 8$ for TN, C/N, pH, and EC; $n = 5$ for textural classes)

HCI	pH	EC (dS m^{-1})	Sand (%)	Silt (%)	Clay (%)	BD (g cm^{-3})	SOC (%)	TN (%)	C/N
HS	8.2 ± 0.1 a	5.6 ± 0.8 a	29.4 ± 7.7 a	33.7 ± 4.0 a	36.9 ± 3.9 a	1.09 ± 0.06 a	1.04 ± 0.14 a	0.045 ± 0.005 a	26.5 ± 3.8 a
SM	8.4 ± 0.1 ab	1.3 ± 0.4 b	45.6 ± 8.3 a	25.8 ± 5.5 a	28.6 ± 2.9 a	1.03 ± 0.02 a	0.88 ± 0.13 a	0.046 ± 0.005 a	18.2 ± 1.4 a
GS	8.6 ± 0.1 b	5.3 ± 0.8 a	38.4 ± 7.0 a	28.0 ± 4.9 a	33.6 ± 2.3 a	1.15 ± 0.01 a	0.39 ± 0.06 b	0.023 ± 0.003 b	18.8 ± 1.8 a

Different letters indicate significant differences among habitats

HCI Habitat of Community Interest, *HS* halophilous scrub, *SM* salt meadow, *GS* glasswort sward

tidal salt marshes and La Pletera salt marsh, since the drier and warmer summers experienced in La Pletera salt marsh, along with soil hypersalinity (which is also increased due to the absence of flooding during summer), would disfavour primary production. Portuguese and Spanish salt marshes in the south-west of the country also have a Mediterranean climate, but tidal movement contributes to avoiding soil hypersalinity, favouring primary production (Carrasco-Barea et al. 2018). These results support the idea that Mediterranean non-tidal salt marshes, at least those habitats dominated by herbaceous and annual species, would be less productive than temperate tidal salt marshes and thus would have a lower carbon sequestration potential.

In general, plant biomass did not change significantly from 1 year to the next in any of the three habitats. This might be caused, at least partially, by the low rainfall recorded in the studied years at La Pletera salt marsh (317 mm y^{-1} and 487 mm y^{-1}, in 2015 and 2016, respectively, when 651 mm y^{-1} was the mean for the last 30 years), with spring and autumn, the two main growing seasons for plants in the Mediterranean Basin, being especially dry. The low rainfall recorded throughout the studied period might also explain the observed reduction in the carbon content of the belowground plant biomass in the three habitats. Indeed, previous works have reported a reduction in the root content of non-structural carbohydrates after a stressful period (Launay et al. 2009; Klein et al. 2014), which has been related to the remobilization of carbon stored in the roots towards other organs to support the main plant functions during or after the stress period (Villar-Salvador et al. 2015). In the case of the glasswort sward, the significant increase in the height of the vegetation from 1 year to the other was mainly due to the appearance of *S. fruticosa*, which had a relative abundance of 21% in 2016. Hence, this result suggests that the glasswort sward might evolve towards a community dominated by *S. fruticosa*, i.e., a halophilous scrub. Interestingly, the carbon content of the aboveground woody tissues of *S. fruticosa* was lower in the glasswort sward than in the halophilous scrub,

concurring with the younger age of the plants in the first habitat (Uri et al. 2012).

Values for litter biomass for the halophilous scrub of La Pletera (571 ± 98 g m^{-2}) were similar to those reported in areas dominated by *S. fruticosa* in other Mediterranean salt marshes (from 383 to 761 g m^{-2}), such as those in the Rhône and Ebro deltas (Berger et al. 1978; Curcó et al. 2002). Conversely, the amount of litter estimated for the salt meadow (419 ± 68 g m^{-2}) was higher than that reported for two Portuguese tidal salt marshes which, despite having a higher aboveground biomass of *H. portulacoides*, had lower annual mean values of litter, ranging from 21 to 120 g m^{-2} (Caçador et al. 2004). This difference probably reflects the importance of the absence of tides on litter accumulation in non-tidal salt marshes, such as La Pletera. Indeed, Caçador et al. (2004) estimated that approximately 86% of the carbon produced in the studied salt marshes was exported out by daily tides. Furthermore, despite the amount of aboveground biomass in the halophilous scrub being much greater than in the salt meadow, they had similar litter values. This could be explained by the slow rate of decomposition of leaves of the most abundant salt meadow species, as has been reported in a parallel study also conducted in La Pletera (Carrasco-Barea et al. 2022).

The higher amount of carbon in the soils of the halophilous scrub and the salt meadow than in the glasswort sward is in accordance with the higher carbon values found in the standing dead aboveground biomass, the belowground biomass and the litter of these two habitats. However, values of soil organic carbon at 0–20-cm depth obtained for the three habitats of La Pletera were much lower than those found at the same soil depth for the Rhône (Hensel et al. 1999) and the Ebro (Curcó et al. 2002) and Po (Scarton et al. 2002) deltas (6.96, 5.01, and 8.93%, respectively), which agrees with the higher belowground plant biomass reported for these salt marshes compared to La Pletera, as discussed previously. In addition, in the present study, the possible overestimation of soil organic carbon produced by the loss-on-ignition method

(Craft et al. 1991) was avoided, since soil organic carbon was quantified using the dichromate wet oxidation method.

Regarding our second hypothesis, we found a higher amount of carbon stored in the soils (at 0–20-cm depth) than in the vegetation of the three habitats of La Pletera, which agrees with the widely accepted idea that in well-preserved salt marshes soils usually store more carbon than vegetation (Dalal and Allen 2008). In fact, while vegetation usually maintains carbon steady stocks, sequestered carbon is mostly buried in the soil (Murray et al. 2010). This is mostly explained by the slow organic matter decomposition that usually occurs in these ecosystems due to the anaerobic conditions that happens in the soil during flooding periods, which avoid the return of carbon dioxide to the atmosphere promoting its accumulation into the soil (Kayranli et al. 2010; Carrasco-Barea et al. 2022). Besides, whereas carbon stays stored in the vegetation for a short-term period (decennial), it stays stored in the soils for long-term periods (millennial) (Duarte et al. 2005). Nevertheless, in the case of the halophilous scrub, the differences between the carbon stored in the vegetation and the soil were not significant, which reinforces the importance of the halophilous scrub vegetation (widely dominated by *S. fruticosa*) as a pool of carbon stored in this salt marsh. Hence, this study highlights the importance of conserving and restoring non-tidal Mediterranean salt marshes to maintain stored carbon pools, which is especially relevant considering that these ecosystems are usually located in very touristic areas, being thus subjected to very high urban pressures (Badosa et al. 2004).

Conclusions

Salt marshes have been largely recognized as ecosystems with a high carbon sequestration potential. However, the results of the present study suggest that, in the Mediterranean Basin salt marshes, the unfavourable climatic conditions during summer (low water availability and soil hypersalinity) can limit below and aboveground plant growth, especially in very dry years. In La Pletera salt marsh, the two habitats with more mature and stable plant communities, the halophilous scrub and the salt meadow (but especially the halophilous scrub), had the highest amount of carbon stored in the vegetation, litter, and soil. The conservation and restoration of these habitats, typical of the Mediterranean coast salt marshes, will contribute to maintain stored carbon pools.

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