Dynamics and drivers of carbon sequestration and storage capacity in *Phragmites australis*-dominated wetlands

Giulia Silan [a,*], Alessandro Buosi [a], Camilla Bertolini [b], Adriano Sfriso [a]

[a] *Department of Environmental Sciences, Informatics & Statistics, Ca' Foscari University of Venice, Via Torino 155, 30172, Venice, Italy*
[b] *We Are Here Venice, 30125, Venice, Italy*

A R T I C L E   I N F O

A B S T R A C T

Coastal wetlands represent important ecosystems performing several functions leading to services. Out of those, the estimation of carbon sequestration and storage capacity is receiving increasing attention for emissions abatement and climate mitigation. *Phragmites australis* - dominated wetlands have the capacity to sequester large amounts of carbon given the large biomass formed annually, however the storage capacity depends on various factors including the environmental conditions that are site-specific. The aim of this study was to develop a method that could be used to quantify the storage capacity, from site-specific plant growth drivers (temperature, light, soil nutrients) and environmental attributes (e.g., particle size of soil). This was achieved with a combination of sampling (above- and below-ground plant biomass, nutrients and carbon content, soil nutrients and carbon at different depths) across the whole Venice Lagoon area where *P. australis* forms habitats under different conditions, using a PCA approach to link biotic and abiotic variables. To upscale the results, a modelling approach in two steps was used, taking first under consideration plant growth under different nutrient availabilities and then simulating the fate of carbon under different conditions (likelihood of material remaining in the area, its decomposition rate, the burial efficiency of soil). The results confirmed a positive effect of nutrient availability, mediated by soil moisture, on plant biomass and storage capacity, in alignment with the model results. Soil type was one the main driver of carbon storage. The knowledge of environmental dynamics and drivers of *P. australis* - dominated wetlands can be useful to support carbon management in order to mitigate climate change. Our model, with a calibration on different environmental conditions, has the potential to predict carbon sequestration and storage enabling it to be used as a management tool for different ecosystems.

1. Introduction

Coastal wetlands represent important environmental ecosystems for human well-being and sustainable development as they perform several ecosystem functions and services e.g., nutrient regulation, supporting biodiversity and sequestering atmospheric carbon dioxide (CO_2) (Gaglio et al., 2022; Gilby et al., 2021; Heckwolf et al., 2021). Acting as efficient natural carbon sinks, wetlands help to offset CO_2 emissions and fight climate change (D'Alpaos and D'Alpaos, 2021). Among ecological services provided by wetlands, carbon storage seems to be one of the most important (Buczko et al., 2022; Brix et al., 2001). The total amount of carbon stored in coastal wetlands is relatively small (10–25 compared to 1500 billion tonnes in soils worldwide) as the total worldwide area of coastal wetlands is small compared with other ecosystem types (Serrano et al., 2019; Pendleton et al., 2012). However, carbon stored in coastal

(and other) wetlands is important because it is stored over a longer time scale compared with most terrestrial soils (wetlands carbon can be stored for hundreds or thousands of years; Hopkinson et al., 2019; Neubauer and Verhoeven, 2019; Serrano et al., 2019).

Coastal wetlands are often dominated by aquatic macrophytes such as *Phragmites, Typha* and *Juncus* (Bertoli et al., 2016) which have significant ecological roles in these ecosystems, for example they play an important role in the detritus food chain supplying an important nutrient source and they improve water quality by removing fertilizers such as nitrogen and phosphorus (Eid et al., 2014; van Dokkum et al., 2002). Aquatic vegetation particularly plays an important role in the carbon cycle being able to sequester and accumulate atmospheric carbon in their organs and tissues, and thereafter in sediments. *Phragmites australis* (Cav.) Trin. ex Steud. is a typical emergent wetland plant and a globally distributed species. The species play a crucial role in

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* Corresponding author.
E-mail address: giulia.silan@unive.it (G. Silan).

maintaining the ecological function of wetlands, providing a variety of ecosystem services, such as water purification, habitat provision and biodiversity conservation (Wang et al., 2022). Specifically, different studies confirm that *P. australis*-dominated wetlands could be regarded as an important carbon sink under an ecosystem services perspective (Brix et al., 2001). *Phragmites australis* can assimilate considerable carbon (Yuckin and Rooney, 2019), indeed the *P. australis*-dominated areas have an annual carbon standing stock that is approximately 3.87 T ha^{-1}, about 2-fold greater than meadow marshes, i.e., wetlands dominated by other sedges and grasses. Under growing concern of climate change due to excessive carbon emission, estimations of carbon sequestration and storage capacity of wetland plants, including *P. australis*, have received increasing attention to support carbon management in order to mitigate climate change (Wang et al., 2022).

Nevertheless, coastal wetlands are some of the most heavily threatened ecosystems (D'Alpaos and D'Alpaos, 2021; Barbier et al., 2011). Wetlands are endangered by several pressures and impacts deriving from human activities (e.g., urbanization, aquaculture or excessive nutrient input resulting in eutrophication, Newton et al., 2020) but also from climate change. These pressures can cause the degradation of the environmental quality and wetland loss (Xi et al., 2021). Therefore, a large part of the stored carbon may be released back into the atmosphere, exacerbating the rise of atmospheric CO_2 concentrations (Bu et al., 2015; Pendleton et al., 2012).

According to the Millennium Ecosystem Assessment (Millennium Ecosystem Assessment, 2005), about the 50 % of inner wetlands were lost during the 20th century in Europe, Northern America and Australia, while habitats and species they host are among those that suffered the most negative impacts. To halt this trend, different policy measures were adopted at international and local levels and knowledge about the carbon storages of different types of wetlands is required (Buczko et al., 2022). The overall global amount of carbon storage is only known with a large margin of uncertainty (Serrano et al., 2019; Duarte et al., 2013). Therefore, it's important to increase the effort to carbon storage and sequestration potential's data collection and considering that data about carbon storage in *P. australis* wetlands worldwide is scarce compared to other coastal wetland types (Buczko et al., 2022). It would be useful to be able to predict the carbon storage capacity of *P. australis* wetlands in different environmental conditions to allow upscaling of protection and restoration where the specific aim is carbon sequestration.

The area selected for the present study was the Venice Lagoon (Northeast Italy). This area is included in several national and international protection plans (e.g., Birds Directive 79/409/CEE). Considering the Habitat Directive (92/43/CEE), the Venice Lagoon is designated as a Special Protection Area (SPA, IT3250046) and the Northern and Central-Southern sub-basin are considered as Sites of Community Importance (SCI, respectively IT3250030 and IT3250031). Coastal lagoons, such as the Venice Lagoon, are ecotones between marine and terrestrial environments, receiving variable amounts of fresh water. These heterogeneous systems are characterized by different physical and environmental gradients (Tagliapietra et al., 2009). The Venice Lagoon constitutes a representative and complex example of a socio-ecological system being characterized by various human activities and valuable ecological elements (Sfriso et al., 2021). Inside the Venice Lagoon there are some areas lined with coastal wetlands dominated by *P. australis*, and this holds true especially for the sites characterized by freshwater inputs (Feola et al., 2022). One of the current threats to the Venice Lagoon ecosystem is its progressive marinization, of which signs are already present (Rova et al., 2023), which could lead to the loss of suitable habitat for *P. australis*. Understanding the potential for carbon sequestration and storage in this site accounting for its heterogeneity and designing a tool to allow its quantification under different scenarios, can be useful in the design of conservation or restoration interventions.

Here, we quantify carbon storage in different *P. australis*-dominated sites considering both *P. australis* biomass and soil. Moreover, we identify environmental drivers of carbon sequestration and storage in *P. australis*-dominated areas. Finally, we create a dynamic growth model of *P. australis* that allows to calculate the potential for carbon sequestration and storage under different conditions.

2. Materials and methods

2.1. Study site

The Venice Lagoon, with a surface of approximately 550 km^2, is one of the largest coastal basin in the Mediterranean Sea. It is connected to the Northern Adriatic Sea by three inlets, and it is characterised by microtidal conditions with a tidal range of ±0.50 m during spring tides (Umgiesser et al., 2004; Solidoro et al., 2004). Moreover, it is also characterised by freshwater inputs from the drainage basin (Ghezzo et al., 2011). The current supply of fresh water from the catchment area is about 30 m^3/s for the entire lagoon (D'Alpaos and Carniello, 2010).

The lagoon is mostly composed of shallow water areas, covering about 75 % of the total surface, with an average depth of 1.2 m (Molinaroli et al., 2009). These areas are connected by a network of natural and man-made channels, whose depth is less than 2 m, leading inwards from the inlets and branching inside the basin (Ghezzo et al., 2010; Solidoro et al., 2004). These shallow water areas are characterised by different gradients of environmental conditions (i.e., salinity, nutrient supply and sediment granulometry). This heterogeneity contributes to creating a complex mosaic of islands, saltmarshes, mud and sandflats, seagrass meadows and man-made structures (Sfriso et al., 2022). Saltmarshes and intertidal and subtidal flats dominate the mosaic of shallow waters in the inner lagoon areas. Reedbeds, dominated by the species *P. australis*, is rare and limited to areas more directly influenced by freshwater (Feola et al., 2018). In this study, plants and environmental sampling was carried out in *P. australis*-dominated sites of the Venice Lagoon, located in the mosaic of shallow waters and in confined saltmarshes, either natural or man-made. Precisely, the selected stations were: 1) Oasi WWF Valle Averto (VA) located within a Special Conservation Area (IT3250030) and Special Protection Area (SPA IT3250046), a wetland of international importance recognized under the Ramsar Convention since 1989. The area includes large stretches of brackish water, reedbeds, wet meadows, hygrophilous woods, canals from the Venice Lagoon and also freshwater input by small canals; 2) Tenuta Conte Marcello (CM), a privately owned area at the mouth of the Dese river, consisting of stretches of brackish water, reedbeds and wet meadows; 3) Porticciolo San Leonardo (Marghera - MA), a small area of reedbeds overlooking the Venice Lagoon, surrounded by channels and an anthropic environment; 4) Lido di Venezia – Alberoni (LA), this *P. australis*-dominated site is a natural wetland connected by a canal to the Venice Lagoon and near to one of the three port-entrance of the Venice Lagoon; 5) Canal Salso (CS), a small area of reedbed overlooking the Venice Lagoon, under the influence of freshwater and urban effluents; 6) Taglio Novissimo (Chioggia - CH), a *P. australis*-dominated wetland located in the southern part of the Venice Lagoon. (Fig. 1).

Plants and sediments sampling.

Fieldwork took place in the period of maximum plant growth, during the vegetative season (June–August) 2022 (Engloner, 2009). We used data about the vegetation cartography of saltmarshes and reedbed of the Venice Lagoon (Cazzin et al., 2009; Ghirelli et al., 2007) and the background knowledge of the working group, to identify *P. australis*-dominated sites. Inside the reedbeds of the six sampling sites, above-ground and below-ground parts of plants (respectively all epigeal and hypogeal structures) were collected by three replications into quadrats of 50 cm^2. Sediment sods with rhizomes and roots were sampled through hand auger (5 cm) from the soil surface to 45 cm depth, sampling limit for the aquifer. Each sample was divided in three sub-samples at 15 cm depth intervals (0–15, 15–30, and 30–45 cm).
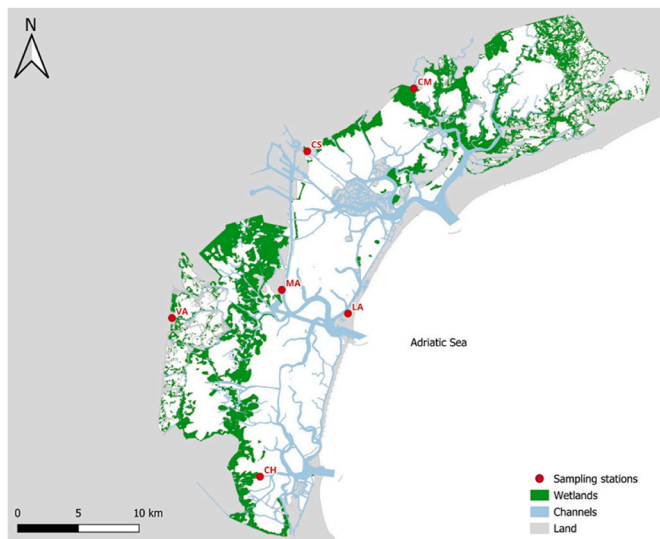
Fig. 1. Map of the Venice Lagoon (NE Italy) with sampling stations (red dots), wetlands (green areas), channels (blue colour) and land (grey areas). (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

2.2. Analysis and data collection

The above-ground plant height (stems and leaves) was measured (in cm). Plant biomasses were weighed in the laboratory using a digital scale to determine the fresh weight (FW). Then plants were oven-dried at 70° for 48 h and weighed again (Garnier et al., 2016) for dry weight (DW) determination.

Carbon (organic and inorganic), nitrogen (total) and phosphorus (organic and inorganic) concentrations were measured both in the plants and in the soil (the visible organic matter was removed). Total carbon (Ctot) was determined directly by CHNS Elemental Analyser (Vario-MICRO, Elementar CHNS by Elementar Italia S.r.l.) after sediment and plant pulverization with a mill and using 0.002 g of soil samples and 0.005 g of plant samples. The inorganic carbon (C_{inorg}) concentration (only in soil) was determined after sample combustion at 440 °C for 2 h using 0.002 g of soil samples for the analysis (Kristensen and Andersen, 1987). So, organic carbon (C_{org}) was determined indirectly as difference between C_{tot} and C_{inorg}. Furthermore, the concentration of total nitrogen (N_{tot}) was measured by the same CHNS Elemental Analyser after an accurate powdering of ca. 0.002 g of soil samples and 0.005 g of plant samples. Total phosphorus (P_{tot}) was determined after sample combustion of 0.3–0.4 g of sample at 550 °C for at least 2 h. Subsequently, the obtained combusted sample was suspended in 50 mL HCl 1 N and sonicated for ca. 30 min. After settling the sample for at least 1 h, 0.5 mL of the supernatant were taken with a graduated gas-chromatographic syringe and brought to exactly 10 mL using volumetric flasks for a final dilution of 1 L, with the result expressed directly in μM. P_{tot} concentration was determined spectrophotometrically by adding the reagents mixed together according to Aspila et al. (1976). The absorbance was read at 885 nm after ca. 10–15 min. Inorganic phosphorus (P_{inorg}) was obtained with the same procedure used for P_{tot} but without combustion at 550 °C. Organic phosphorus (P_{org}) was determined by difference. All samples were analysed in duplicate and analyses were replicated in two different days to obtain an accuracy >95 %. Otherwise, the analyses were repeated until the coefficient of variation (standard deviation/mean) between replicates was <5 %.

Soil carbon storage, grain-size (sand and silt),density (g cm^{-3}), moisture (%) and salinity (PSU) of each subsample were also determined to characterize the sites according to Sfriso et al. (2005). The

percentage of fines (fraction ≤63 μm) was obtained by wet sieving approx. 50 g of dried sediment throughout Endecotts sieves (ENCO Scientific Equipment, Spinea, Italy), after removing shell fragments (Sfriso et al., 2005). Sediment density (g cm^{-3}) and moisture (%) were determined by gravimetric method weighting the sediment before and after desiccation at 110 °C (Sfriso et al., 2005).

Salinity (PSU) measurements were carried out by drying soil samples at 70 °C for 36 h, then they were pressed and homogenized. Twenty grams from each sample were then mixed with 100 g of distilled water and the solution was allowed to reach an equilibrium salt concentration for 12 h. Salinity was evaluated by measuring conductivity (WTW MultiLine p4 Conductivity meter; Silvestri et al., 2005).

According to Howard et al. (2014), the total soil carbon storage within each station was determined by the amount of carbon within a defined area and soil depth. The total soil carbon content was determined according to the following formula:

Soil carbon stock (g cm^{-3}) = % soil Corg x soil dry density (g cm^{-3}) * soil depth * ha and reported in tonnes C ha^{-1}.

2.3. Statistical analyses

2.3.1. PCA

The influence of environmental drivers on the *P. australis*-dominated sites, was determined by applying the Principal Component Analysis (PCA) to the total matrix composed by the 6 sites where the following soil parameters were recorded (C_{org}, C_{inorg} (mg g^{-1}), P_{org}, P_{inorg} (μg g^{-1}), N_{tot} (mg g^{-1}), moisture (%), salinity (PSU), silty and sandy fractions (%); plant parameters (i.e., above- and below-ground biomass (g DW m^{-2}); plant height (cm), leaves, stem, rhizome and root C_{tot}, N_{tot} and P_{tot} (mg g^{-1}) concentrations, and leaves N:P weight ratio). The analysis was performed using CANOCO Software (v. 5. TerBraak and Šmilauer, 2012).

2.3.2. Model

A dynamic growth model of *P. australis* described in Asaeda and Karunaratne (2000) was coded in R, this model can simulate the growth dynamics of a monospecific stand using daily temperature and irradiance as forcing functions, the model simulates biomass of five state variables: shoots, inflorescences, roots, old and new rhizomes. Advances on the modelling of plant growth dynamics with the same modelling approach included the addition of a 'nutrient availability constant' parameter (*Knp*) that modulates the effects of nutrients on the photosynthetic rate and was tested for *Spartina alterniflora* (Zheng et al., 2016). In this study we used the same approach for *P. australis* simulating multiple conditions, since environment inhabited by this species can have a big variability in nutrient concentrations: *Knp* was made to vary between 0.1 and 1 with a 0.1 step length, where 0.1 limits the maximum specific net photosynthesis rate to 10 % while 1 signifies a not-limited condition (100 % of maximum specific net photosynthesis rate). Since the plant growing period varies depending on the climatic region (Asaeda and Karunaratne, 2000), the shoot emergence was set as Julian day 90 (end of March) according to species knowledge (Engloner, 2009). To avoid confounding effects, the starting rhizome biomass, required to initiate shoot biomass growth, was set at 3000 g DW m^{-2} according to Asaeda and Karunaratne (2000) simulation in the Czech Republic (similar latitude). Environmental forcings required for the model, namely air temperature at 2 m (°C) and global irradiance (W m^{-2}), were obtained from ARPAV at the station Chioggia-Sant'Anna (Latitude 45.218127, Longitude 12.283051). Data spanned the years 2000–2020, but in order to simulate a 'typical' year, each day of the twenty-year time series was averaged to obtain the two-time series necessary to use as inputs for the model. The model output was a daily time series of biomasses (g DW m^{-2}) of the different plant parts: above-ground (shoots, panicles) and below-ground (roots, rhizomes, new rhizomes).

To get an approximate estimate of the nutrient availability in each

site, the model was compared to the empirical data described above. To compare the same time period of collection, from the output the days when the sampling campaign took place (31/05 until 31/07) the below- and above-ground biomasses were averaged. Finally, to calculate the potential carbon sequestration the mortality rates (g DW m^{-2}) of each pool of biomass arising from the dynamic model described above were summed over the whole year and multiplied by the carbon content (%) of above- and below-ground parts, estimated empirically as described above. Because carbon sequestration depends on the decomposition rate of the dead material (dr), the burial efficiency of the soil (BE) and the proportion of the above-ground dead material that is retained (i.e. not blown or washed away) (pr), simulations with different values of these parameters (dr: ranging from 20 % to 100 % in 10 % increment; BE either 1 % or 30 %, representing sandy or muddy shallow coastal sediments (Burdige, 2007), pr ranging from 1 % to 100 % in 10 % increments) were run to estimate the potential for sequestration under these different environmental conditions, which are assumed to be representative of sites typically occupied by *P. australis*. PCA analysis was then run to visualize the way in which these parameters influence carbon sequestration.

3. Results

3.1. Sediment parameters

All sites had mainly sandy sediments, especially MA (96.0 % ± 0.57), LA (93.2 % ± 1.24) and VA (82.5 % ± 9.19), compared to CM, CS, CH where the silt fraction prevailed (45.4 ± 2.91, 32.0 ± 6.07 and 31.4 % ± 4.66, respectively; Table 1). Soil moisture was the highest at CM (58.1 % ± 6.00) and the lowest at MA (3.89 % ± 0.30). Salinity ranged from 0.21 ± 0.01 at VA to 5.32 ± 0.02 at CH. In the other stations salinity was in the range 1.12–2.29 (±0.02 and ± 0.02 respectively). Soil carbon concentration was very different ranging from 44.5 ± 3.63 mg g^{-1} DW at VA to 98.6 ± 2.99 mg g^{-1} DW at LA. However, the highest C_{org} was recorded at CM and CS with 63.0 ± 17.6 and 44.8 ± 2.40 mg g^{-1} DW and the lowest at VA with 7.41 ± 9.39 mg g^{-1} DW. In the other stations C_{org} ranged between 14.1 ± 7.71 and 16.2 ± 6.40 mg g^{-1} DW. The highest N_{tot} (4.93 ± 1.46 mg g^{-1} DW) and P_{tot} (1037 µg g^{-1}DW) were found at CM and CS. In contrast the lowest N_{tot} was recorded at LA (0.29 ± 0.18 mg g^{-1} DW) and MA (0.37 ± 0.12 mg g^{-1} DW) and the lowest P_{org} at LA (75 µg g^{-1} DW, only).

3.2. Phragmites australis characteristics

The mean plant height was 129 ± 63 cm (mean ± sd), with the highest values at CS (231 ± 29 cm) and VA (176 ± 30 cm) (Table 2). The lowest height was recorded at MA (67 ± 18 cm) and LA (78 ± 13 cm). These data confirmed the biomass values of the above-ground parts. Indeed, the highest biomass was found at CS (4331 ± 242 g DW m^{-2}) and VA (2471 ± 234 g DW m^{-2}) and the lowest biomass at MA (986 ± 7

Table 2

Height and above- and below-ground biomass of Phragmites australis in the six stations. Mean value ± standard deviation.

Station	Plant height	Biomass		
		Above-ground	Below-ground	Total
	cm ± std	g DW m^{-2} ± std		g DW m-2
VA	176 ± 30	2471 ± 234	4213 ± 90	6684
CM	117 ± 33	1706 ± 72	1819 ± 76	3524
MA	67 ± 18	986 ± 75	200 ± 39	1186
LA	78 ± 13	1119 ± 135	1293 ± 98	2412
CS	231 ± 29	4331 ± 242	205 ± 33	4536
CH	104 ± 14	522 ± 67	419 ± 41	941
mean	129	1856	1358	3214
std	63	1386	1544	2182

g DW m^{-2}) and CH (522 ± 67 g DW m^{-2}).

The mean nutrient concentrations in the different plant regions (leaves, stems, rhizomes and roots) in all the stations are reported in Table 3. The mean values of C, N and P in the entire plants and in the whole stations were 437 (C), 9.80 (N) and 1.59 (P) mg DW g^{-1}.

On average, in the six stations, leaves, stems and rhizomes showed similar carbon concentrations (440 ± 11.0–450 ± 6.93 mg g^{-1} DW) whereas roots had slightly lower values (411 ± 15.7 mg g^{-1} DW) although the differences among stations were higher. In contrast, nitrogen was approximately three times higher (23.7 ± 5.68 mg g^{-1} DW) in leaves than in the other plant regions. No information for the concentration of phosphorus in the different plant regions is available. The mean N:P ratio on weight basis was 14.9 ± 2.13.

3.3. PCA

Considering sediment parameters as the environmental drivers that positively influenced *P. australis*-dominated sites, the 1st component of the PCA analysis (Fig. 2), captured approx. 74 % of the total variance and was highly correlated with soil moisture (%). The 2nd component explained approx. 18 % of the total variance, whose positive contributions were mainly soil P_{inorg}, P_{org} and N_{tot} concentrations. Moreover, the ordination showed that CS was characterised by soil P_{inorg} and P_{org} and in a limited measure by soil N_{tot} and C_{org}. In contrast, CH and in a minor extent LA and MA were related to salinity, the sand soil content and C_{inorg}. CM but also LA and VA were mainly characterised by soil moisture.

3.4. Carbon storage

The mean soil amount of C_{org} stock (Fig. 3) in all the stations was estimated to be approx. 92.8 ± 6.39 tonnes ha^{-1} in the 45 cm soil top layer. It ranged from 146.1 (CM) to 49.9 (VA) tonnes ha^{-1} and in some

Table 1

Sand, Silt, Moisture salinity, Organic Carbon (C_{org}), Inorganic Carbon (C_{inorg}), Total Carbon (C_{tot}), Total Nitrogen (N_{tot}), Organic Phosphorus (P_{org}), Inorganic Phosphorus (P_{inorg}) and Total Phosphorus (P_{tot}) of soil in the six stations. Mean value ± standard deviation.

	Sand	Silt	Moisture	Salinity	Corg	Cinog	Ctot	Ntot	Porg	Pinog	Ptot
	%	%	%	psu	mg g^{-1} DW	mg g^{-1} DW	mg g^{-1} DW	mg g^{-1} DW	µg g^{-1} DW	µg g^{-1} DW	µg g^{-1} DW
VA	82.5 ± 9.19	17.1 ± 9.35	29.3 ± 5.53	0.21 ± 0.01	7.41 ± 9.39	37.1 ± 5.04	44.5 ± 3.63	2.33 ± 3.16	160	273 ± 8.67	434 ± 14.7
CM	50.9 ± 4.85	45.4 ± 2.91	58.1 ± 6.00	2.29 ± 0.02	63 ± 17.6	24.8 ± 16.4	87.7 ± 5.06	4.93 ± 1.46	421	486 ± 4.52	908 ± 36.8
MA	96 ± 0.57	3.5 ± 0.59	3.89 ± 0.3	0.28 ± 0.01	14.1 ± 7.71	46.8 ± 6.77	60.9 ± 0.84	0.37 ± 0.12	179	352 ± 13.9	530 ± 21.9
LA	93.2 ± 1.24	6.5 ± 1.45	23.3 ± 2.82	1.91 ± 0.01	16.2 ± 6.4	82.5 ± 8.47	98.6 ± 2.99	0.29 ± 0.18	75	318 ± 16.2	394 ± 21.1
CS	59.4 ± 3.89	32 ± 6.07	14.6 ± 0.57	1.12 ± 0.02	44.8 ± 2.4	48.4 ± 0.65	93.2 ± 2.62	4.15 ± 0.45	399	638 ± 9.89	1037 ± 2.09
CH	64.4 ± 3.99	31.4 ± 4.66	27.3 ± 4.81	5.32 ± 0.02	15.7 ± 3.9	42.6 ± 4.87	58.2 ± 1.39	0.95 ± 0.17	148	396 ± 15.8	544 ± 33.9
mean	74.4	22.7	26.1	1.9	26.9	47.0	73.6	2.20	230	411	641
std	18.8	16.4	18.3	1.9	21.9	19.4	22.1	1.99	144	133	266

Table 3
Height nutrient contents in the different plant regions and leaf N:P on weight basis. Mean value ± standard deviation.

Station	Carbon					Nitrogen					Phosphorus	
	Leaves	Stems	Rhizomes	Roots	mean	Leaves	Stems	Rhizomes	Roots	mean	Leaves	N:P weight
	mg g^{-1} DW					mg g^{-1} DW					mg g^{-1} DW	
VA	444 ± 1.73	453 ± 0.97	437 ± 1.58	417 ± 1.38	438	25.8 ± 0.24	5.1 ± 0.17	4.7 ± 0.29	9.81 ± 0.1	11.4	1.58 ± 0.02	16.3
CM	443 ± 1.98	446 ± 1.34	433 ± 0.96	413 ± 2.37	434	26.1 ± 0.47	6.8 ± 0.19	3.8 ± 0.14	6.5 ± 0.17	10.8	2.06 ± 0.01	12.7
MA	458 ± 2.11	443 ± 0.85	445 ± 2.74	422 ± 0.85	442	17.9 ± 0.12	7.2 ± 0.23	3.91 ± 0.36	6.48 ± 0.19	8.9	1.2 ± 0.03	14.9
LA	448 ± 2.15	448 ± 1.01	437 ± 2.62	406 ± 3.14	435	28.8 ± 0.38	12.3 ± 0.35	12.9 ± 0.38	13.6 ± 0.11	16.9	1.85 ± 0.01	15.6
CS	443 ± 1.99	448 ± 1.38	460 ± 2.86	425 ± 2.84	444	28.1 ± 0.27	7.3 ± 0.41	4.5 ± 0.25	14.9 ± 0.27	13.7	1.6 ± 0.09	17.6
CH	443 ± 3.19	462 ± 0.97	429 ± 1.94	382 ± 1.97	429	15.2 ± 0.11	3.5 ± 0.19	5.1 ± 0.44	7.5 ± 0.13	7.8	1.26 ± 0.03	12.1
mean	446	450	440	411	437	23.7	7.03	5.82	9.8	11.6	1.59	14.9
std	5.93	6.93	11,0	15.7		5.68	2.97	3.5	3.68		0.33	2.13
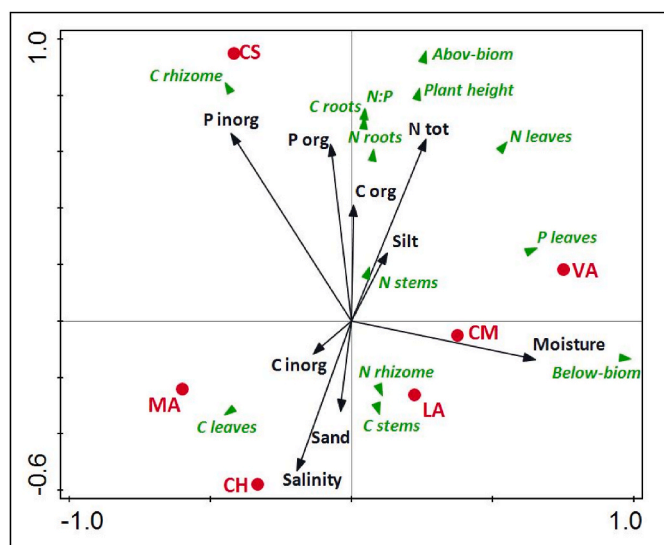
Fig. 2. PCA representing the relationship between environmental drivers (black text and arrows) and plant characteristics (green text and arrows) of each sampling stations (red text). (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

stations (VA, MA and CS) it decreased with depth. On average, the amount recorded in the surficial layer (0–15 cm) was the highest (37.9 tonnes ha^{-1}) whereas the lowest stock (23.1 tonnes ha^{-1}) was found in the deepest layer (30–45 cm).

The highest stock in surface sediments (0–15 cm) was recorded at CM (59.6 Tonnes ha^{-1}), while the lowest concentration was found at CH (20.0 Tonnes ha^{-1}). Corg concentration at VA in the deepest (30–45 cm) soil layer was particularly low (2.62 Tonnes ha^{-1}).

The mean *P. australis* C$_{org}$ stock in all stations was 14.1 ± 9.6 tonnes ha^{-1}, i.e. 8.34 ± 6.28 tonnes ha^{-1} in the above-ground plant part and 5.77 ± 6.60 tonnes ha^{-1} in the below-ground plant part. The highest plant C$_{org}$ value was found at CM and MA (29.1 and 20.4 tonnes ha^{-1}, respectively). The lowest ones at VA and LA (4.12 and 5.30 tonnes ha^{-1}, respectively). High differences between stations and the above-below region were recorded. Indeed, C$_{org}$ in above-ground *P. australis* was very high at CM (11.1 tonnes ha^{-1}) and almost negligible at LA (2.34 tonnes ha^{-1}). Similarly, in the below-ground region it ranged from 19.6 1 tonnes ha^{-1} at MA and 0.83–0.86 tonnes ha^{-1} at CS and MA, respectively).

3.5. Model

3.5.1. Phragmites australis growth

The predictions from the dynamic model are shown in Fig. 4. The above-ground biomass started to increase around day 91 and peaked at day 224. The minimum and maximum biomass that would be reached is 800 and 8000 g DW m^{-2} with the nutrient constant set at 0.1 and 1.0,
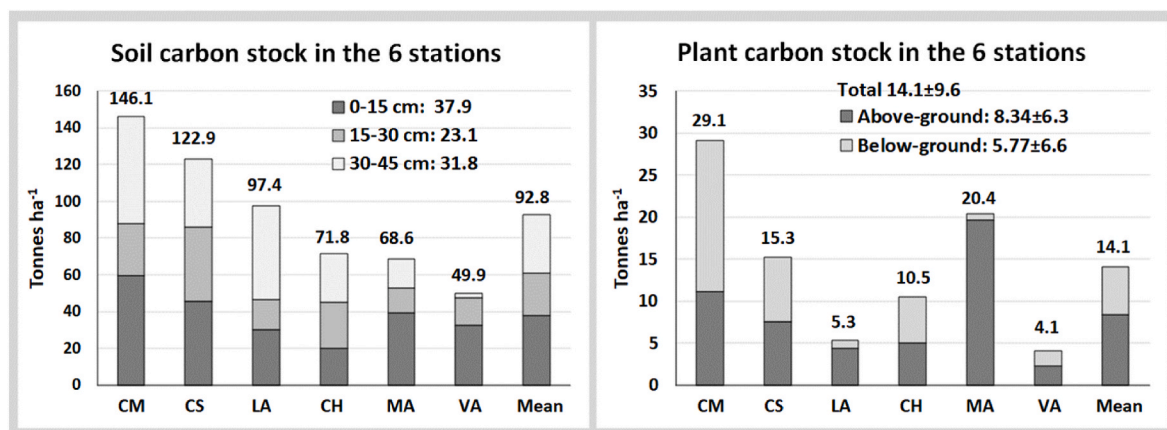
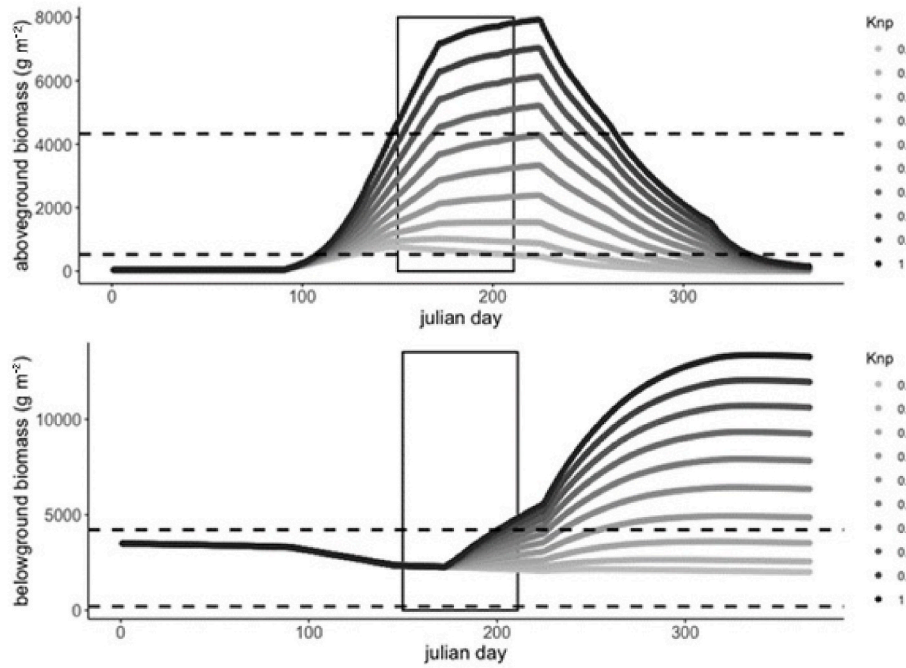**Fig. 3.** Plant and Soil carbon stock in the six stations.

Fig. 4. Above- and below-ground plant biomasses at each time step of *P. australis* in a typical year according to different nutrient availability constants. Horizontal dotted lines represent values as measured in the sampling campaign.

respectively. The infield biomass values (sampling dates in rectangle) ranged between 200 and 4200 g DW m^{-2} (dashed lines). They are indicative of a nutrient constant between 0.1 and 0.7.

With regards to the below-ground biomass, the model predicted the new plant onset at day 172 with peaks ranging from 350 to 13400 g DW m^{-2} (Knp 0.1–1). Growth was stabilized at day 336. The highest values were reached outside the dates of the sampling campaigns, and the model predictions in the sampling dates were within the growth range, but the nutrient constant had larger effects during the latter part of plant growth.

The mortality time of the above-ground parts showed the highest

peak around day 315. A secondary peak was observed around day 270. Mortality rates reached at the highest peak accounted for 128 g DW m^{-2} d^{-1}. Below-ground mortality rates peaked around day 234, with a loss of 1.5 g DW m^{-2} d^{-1} (Fig. 5).

3.5.2. Carbon

The potential carbon sequestration at the end of a year growth ranged from 2.70 to 25.60 tonnes C ha^{-1}. It was based on different nutrient constants, which could range from 0.002 to 7.95 tonnes C ha^{-1} if environmental conditions are considered. Burial efficiency of soil and decomposition rates would have the largest impacts on the actual carbon
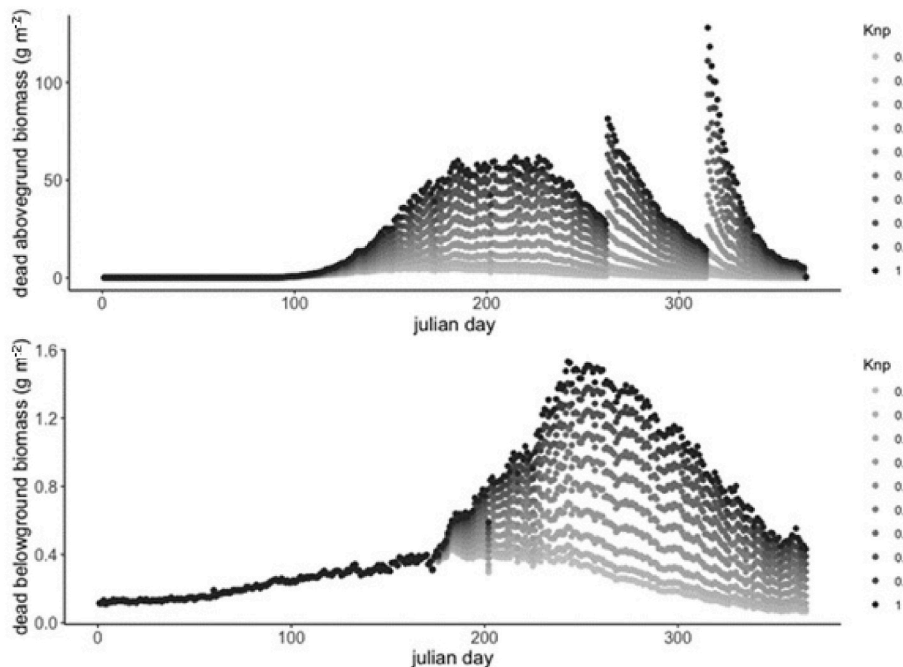

Fig. 5. Dead above- and below-ground plant biomasses at each time step in a 'typical' year.

storage, followed by the proportion retained (Fig. 6).

4. Discussion

Phragmites australis-dominated wetlands act as an important carbon sink under an ecosystem service perspective assimilating carbon from atmosphere (Soetaert et al., 2004; Brix et al., 2001). Our results allow us to demonstrate that some environmental drivers and some plant characteristics have important implications for carbon sequestration and storage capacity, confirming the increasing attention in carbon estimation that can mitigate climate change (Wang et al., 2022). Moreover, the growth model is in line with carbon storage estimation and it is linked to PCA results, confirming the importance of nutrient availability for carbon accumulation but also the dependence on other environmental parameters (e.g. soil type) for sequestration leading to storage.

4.1. Summary statistics and PCA

Among environmental drivers, soil moisture turns out to be the most influencing on *P. australis* wetlands. Sites influenced by soil high moisture (CM, and in a minor extent VA, showed the highest value of soil moisture) are also characterised by high values of plant below-ground biomass. Moreover, VA site is directly correlated to the presence of higher values of nutrients such as phosphorus and nitrogen than other sites. These data confirm the positive relationship between nutrient supply and biomass and, in addition, it is possible to suppose a positive effect of soil moisture on plant biomass production (Saltonstall and Stevenson, 2007; Bastlová et al., 2004). Furthermore, according to Karunaratne et al. (2004, 2003), *P. australis* rhizomes, that determine most of the below-ground biomass, do not grow during spring. The model output shows that rhizome biomass decreased from April to May because of depletion of stored reserves, while a steady increase of rhizome biomass was predicted from May to August, confirming the importance of a nutrient rich environment (within the expected input into wetlands; Sfriso et al., 2021) to the growth of below-ground biomass.

In addition, several findings have demonstrated both the positive effect of nutrient supply on biomass production and the negative effect of increasing salinity (below-ground and above-ground; Cho et al., 2017; Engloner, 2009). This study highlights that *P. australis* at VA was characterised by high values of below-ground biomass and low values of soil salinity, while *P. australis* at CS was characterised by high values of above-ground biomass and high values of soil nutrients. Moreover, even if CM showed high nutrient values, it also showed high values of soil salinity that limits plant growth. This relationship between nutrients and biomass is also well expressed in the version of the model proposed here. The comparison of the sampled biomass with the model outputs suggests that sites have a nutrient limitation constant between 0.1 and 0.7 knp. The negative effect of soil salinity however is not here considered: a next step could be done with a further improvement to the model adding the salinity effects on the growth initiation as modelled by Soetaert et al. (2004). The Venice Lagoon is experiencing a N and P decrease in surface sediments (Sfriso et al., 2021) which are lower than in other lagoons. However, it should be noted that the model input forcings aimed at simulating a general year of temperatures and irradiances, and all simulations started with the same rhizome biomass, from which shoots arise. This was done to allow for comparisons of likely effects of other environmental drivers, rather than be an exact representation of reality, as there are carry over effects from previous years of different below-ground biomass (primarily made of rhizomes). In the sites sampled in this study those differences were up to 20-fold (200–4331 g DW m^{-2}). Moreover, as suggested by Engloner (2009), it seems to be clear that the increase of salinity diminishes plants growth, especially plants height, whereas nutrient increasing (also only nitrogen) generally favour plant production.

Concerning the relationships between N, P and N:P weight ratios it depends on the set of nutrient conditions to which plants are exposed and on the plasticity of a species in N and P (Güsewell, 2004). Indeed, variation in N:P ratios in *P. australis* is primarily determined by P variation because N is relatively stable, as is usually observed in graminoid species (Güsewell, 2004). Furthermore, N and P concentrations in *P. australis* were positively correlated with each other confirming the fact that when a species is sampled at different field sites the same sites tend to be N and P-rich and non-nutritional factors (e.g., shade, drought)
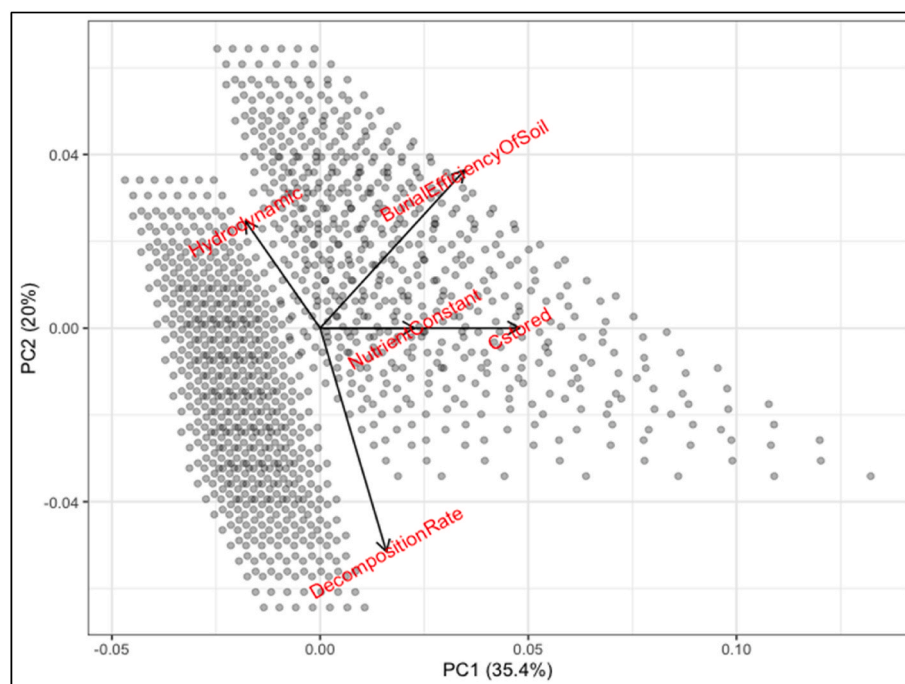

Fig. 6. PCA representing potential carbon stored in the different simulations (dots), direction of increase given by C stored and influences of drivers (arrows and red text). (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

have similar impacts on N and P (Güsewell, 2004).

On the other hand, below-ground biomass allocation increases in response to deficiency of both N and P, even if the effect of N is usually stronger (De Groot et al., 2003). As a result, plants with a high N:P ratio normally allocate less biomass to the under-ground part than plants with the same growth rate but a lower N:P ratio (Güsewell and Bollens, 2003). This result is not reflected in the model as it uses a constant of nutrient limitation (Knp) that influences the above-ground biomass only. Finally, considering soil grain-size, sites with a predominant sandy sediment have low values of above- and below-ground biomass (MA and LA), while sites with a predominant silty sediment have high values of above- and below-ground biomass (CM and CS sites). Furthermore, CM had significant soil moisture, while CS had significant soil nutrient amounts.

4.2. Carbon storage and sediment sequestration

The C-storage capacity of salt marshes, seagrass meadows and mangroves exceeds that of green (terrestrial) forest ecosystems because of the combination of high ecosystem productivity, high potential for sedimentation of organic matter originating from the ecosystem itself (autochthonous) and from the surroundings (allochthonous), and the refractory nature of part of the organic matter and waterlogged, anaerobic conditions limiting decomposition (Mcleod et al., 2011). In this contest, as reported by Serrano et al. (2019) the C-sequestration capacity within 1 m soil top layer of salt marsh, seagrass and mangrove ecosystems were in the ranges 4.8–87.3, 48–112 and 5–10.4 million tonnes C y^{-1}, respectively. In another paper (IPCC et al., 2013) the carbon storage by tidal salt marshes was evaluated to be approx. 255 tonnes ha^{-1}, with an absorption of 935 CO_2 tonnes ha^{-1}. Furthermore, for the river ecosystem, Buosi et al. (2021) calculated that the total mean ecosystem C_{org} storage in a Northeastern Italy river was 95.2 ± 13.8 tonnes C ha^{-1}. An amount of 86.6 ± 14.5 tonnes C ha^{-1} was stored in the sediments whereas submerged aquatic macrophytes retained from 7.0 to 10.9 tonnes C ha^{-1}, accounting for approx. 10 % of the total C_{org} sediment storage. The results obtained in this study were lower than those of other ecosystems, such as mangrove forest reported in Stringer et al., (2015), where the carbon stock ranged from 373 to 620 tonnes C ha^{-1}, instead they were within the average value recorded in tidal salt marsh and seagrass ecosystems (Chen and Lee, 2022; Serrano et al., 2021; Fourqurean et al., 2012). However, the values of carbon storage and the carbon stock in *P. australis* were lower than those of mangroves (Thura et al., 2023), considering both the many environmental factors that drive carbon trends and the different carbon content in organs plants and in plants life forms (Ma et al., 2018). Moreover, C-storage in soil of the different sampling sites, was strongly affected by its characteristics such as moisture, nutrient availability and grain-size. Improving soil nutrients such as nitrogen (N) and phosphorus (P) enhances net primary production and hence plants biomass that entails more C-storage also in sediments (Were et al., 2019).

Plant C-sequestration, without considering the dead biomass and its fate, as most of the above-ground biomass dies annually, can be very high. The range obtained with the model (2.70–23.50tonnes C ha^{-1}), primarily driven by C stock in the dead above-ground biomass (2.35–24.95 tonnes C ha^{-1}) is in line with the C stock in the sampled biomass (above-ground parts: 2.34–19.60 tonnes C ha^{-1} live below-ground part: 0.83–18.00 tonnes C ha^{-1}). In this study the above metric is a good indicator of carbon accumulation rates, when calculating the actual annual potential for C sequestration (i.e., the carbon entering the carbon pool) it is important to consider environmental factors that would remove the carbon from the local pool (e.g. washed away, entering the trophic chain or returning to the atmosphere). To increase carbon storage there is a need for high decomposition rates, high soil burial efficiency (i.e., mud vs sand dominated marine soils; Burdige, 2007) and low hydrodynamic forces to avoid the biomass displacement. Different simulations ran with a range of parameters

showed that C-storage can be largely diminished, going down to 0.002 g tonnes C ha^{-1} y^{-1} in the worst scenario (low decomposition rates, a highly hydrodynamic sandy site). These values cannot be corroborated with the field dataset, which considered total rather than yearly sequestration and are simulated with a fixed rhizome starting biomass, however the overall carbon storage shows high soil C_{org} stock at CM and CS which had also relatively high above-ground biomasses (1st and 3rd highest value). VA which had the 2nd highest biomass showed a low C_{org} stock in the presence of a high percentage of sand in the soil, which would result in low burial efficiency. In order to estimate C burial is important to have some information on the site in terms of temperature, irradiance and nutrient availability necessary for plant growth, but also to know the soil grain-size. In *Phragmites* habitats, especially in dense beds, hydrodynamics may not be too much of an issue as the strands themselves may help attenuating its loss (Reef et al., 2018; Temmerman et al., 2005). In the case of the Venice Lagoon decomposition rates could also be assumed to be similar between the different areas, although not tested specifically.

4.3. Concluding remarks

This study highlights and confirms *P. australis* - dominated wetlands are an efficient natural carbon storage. Accordingly, the conservation of *P. australis* wetlands and the knowledge of the environmental dynamics of carbon sequestration and storage are essential to support carbon management in order to mitigate climate change. Specifically, more research is needed on the carbon fluxes from wetlands that are freshwater - dominated to determine if they are net carbon sinks under certain conditions. The analysis of soil characteristics for an optimal carbon storage capacity, underlines the significant role of nutrient availability, soil moisture and grain-size. Moreover, these characteristics act as important drivers on plant biomass production that improve the C-storage in sediments. *Phragmites australis* has the capacity to assimilate carbon and nutrient and according with widespread studies it is possible to conclude that the increase of nutrients loads lead to an increase in total plant biomass.

Therefore, to understand the role of *P. australis* and use it for global climate mitigation actions, it is useful to consider site specific environmental conditions at the project sites. Our results confirm their essential role in C-storage and eventual sequestration. Data collected across a heterogeneous site allowed to work on a model that could be useful towards a scaling up approach. The model presented in this study can simulate the C-sequestration under different site-specific conditions and can be implemented in different areas assuming known nutrient availability, starting rhizome biomass and conditions related to the retention and degradation of dead biomass (e.g., hydrodynamic regime, particle size, the presence of remineralizing bacteria). If these conditions are unknown, the model can still be utilised, as done in this case, to provide a range of possible values within which it would be possible to operate based upon assumptions of these conditions.

CRediT authorship contribution statement

Giulia Silan: Writing – original draft, Methodology, Investigation, Formal analysis, Conceptualization. **Alessandro Buosi:** Writing – original draft, Methodology, Investigation, Formal analysis, Conceptualization. **Camilla Bertolini:** Writing – original draft, Methodology, Investigation, Formal analysis. **Adriano Sfriso:** Writing – original draft, Supervision, Resources, Project administration.

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.

Data availability

Data will be made available on request.

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