MODELLING THE EFFECTS OF GLOBAL TEMPERATURE INCREASE ON THE GROWTH OF SALT MARSH PLANTS

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Abstract. Gradual increases in temperature and atmospheric CO_2 concentrations have resulted from the increased human use of fossil fuels since the beginning of industrial activity. In coastal wetland ecosystems, salt marshes constitute important habitats because they play important ecological roles, acting as carbon sinks by capturing atmospheric CO_2 and storing it in living plant tissue. Ecological models are important tools for understanding the results of anthropogenic impacts on a global scale. Global warming poses threats to salt marshes through different effects, e.g., increases in sea level. The objectives of this study were i) to assess how temperature increases will influence the growth of salt marsh plants, ii) to infer the carbon budget of salt marshes under temperature increase scenarios and iii) to predict how salt marsh plants will keep pace with increases in sea level. These goals were achieved by developing growth models of three different plants (*Spartina maritima*, *Scirpus maritimus* and *Zostera noltei*) found in the Mondego estuary. Models were developed for C_3 and C_4 plant species. The results suggest that a temperature increase enhances the aboveground biomass of salt marsh plants. According to the predictions of the models, the sedimentation rate of *S. maritima* and *Z. noltei* can keep pace with increases in sea level, but this is apparently not the case for *S. maritimus*. If *S. maritimus* disappears from the Mondego estuary, the carbon sequestration ability of the system should decrease due to the loss of active plant tissue. This conclusion is based on the fact that *S. maritimus* accumulated more than 80% of the total carbon sequestered in the tissues by the three studied species.
Keywords: *plant growth model, sea level increase, sedimentation, salt marsh, estuaries*

Introduction

Because of increasing human fossil fuel use since the beginning of intensive industrial activity (Houghton, 1999), the world has experienced an increase in atmospheric CO_2. It is widely believed that anthropogenic additions of CO_2 to the atmosphere are contributing to increase surface temperatures worldwide, a phenomenon known as the ''greenhouse effect'' (Bluemle *et al.,* 1999). IPCC (2007) reports show that the global temperature increased approximately 0.3 °C per decade from 1979 to 2005. Coastal wetlands such as salt marshes are excellent carbon sinks, as they withdraw CO_2 from the atmosphere and store it in living plant tissue (Williams, 1999). Salt marshes reduce the rates of greenhouse gas emissions (Magenheimer *et al.*, 1996) and have a carbon sequestration capacity per unit area approximately one order of magnitude higher than other wetland systems (Bridgham *et al.*, 2006), with the potential to sequester carbon continuously over thousands of years (Brevik et al, 2004). In

addition to their carbon storage capacity, salt marshes are key areas for estuarine systems because of their role in primary production and nutrient regeneration (Caçador et al., 2009). They represent one of the most productive ecosystems on the planet (Lefeuvre et al., 2003). However, global warming can threaten salt marsh areas through, e.g., increases in sea level. Salt marsh ecosystems play a vital role in the dissipation of wave energy, accretion of sediment and filtration of nutrients and as habitats supporting commercially important fisheries (Mudd et al. 2009). These ecosystems are vulnerable to changes in sea level (Cundy & Croudace, 1996, Rybczyk & Cahoon, 2002), and sea level increases have become a severe threat to coastal zones and estuaries at low elevations (Vandenbruwaene et al. 2011). It is recognised that many marshes are able to keep pace with increases in sea level (Friedrichs and Perry, 2001); the response of coastal marshes to relative increases in sea level depends upon their ability to maintain their relative elevation through sedimentation (Reed, 1990). IPCC (2007) reports show that the most pessimistic prediction for sea level change is an increase of approximately 0.97 cm per year, which will endanger certain areas around the world that are influenced by the tides, including, in particular, the Mondego salt marsh. Ecological models have been used to clarify the effects of anthropogenic impacts on a global scale by integrating processes related to the biota of the ecosystem in its conceptual structure (Fragoso Jr., et al. 2009). Accordingly, an ecological model focuses on the objects of interest for a considered and well-defined problem. There can be many different ecological models of the same ecosystem, as the model version is selected according to the goals of modelling (Jørgensen & Fath, 2011). Because *Spartina maritima, Scirpus maritimus* and *Zostera noltei* together occupy approximately 50% of the salt marsh vegetation of the Mondego estuary (Neto, unpublished data), these species were selected as the focus of the present study. Our goal was to examine the influence of temperature increase on the carbon accumulation of the salt marsh area of the Mondego estuary. Specifically, our objectives were to investigate how temperature increase influences the growth of salt marsh plants (*Spartina maritima*, *Scirpus maritimus* and *Zostera noltei*) and their carbon storage capacity. Furthermore, we attempted to estimate whether the sedimentation rate of the three salt marsh plants can keep pace with the increase in sea level.

Materials and methods

Study site

The Mondego estuary (Fig. 1) is located on the Portuguese Atlantic coast (40°08 N, 8°50 W) (Marques and Nogueira, 1991). The estuary is approximately 8.6 km^2 in area, and its upstream limit extends up to 21 km from the mouth of the estuary (Teixeira et al., 2008). The final portion of the estuary (approximately 7 km) is divided into two arms (north and south) by Murraceira Island (Marques et al., 2003). The sample sites for this study (Fig. 1) were located in the south arm of the estuary. The south arm is shallower than the north arm (2–4 m during high tide) and is characterised by large areas of intertidal mudflats (almost 75% of the area) (Neto et al., 2008). The sediments of the south arm contain a high percentage of silt and clay, and the area is considered to be a rich estuarine habitat in terms of productivity and biodiversity (Marques et al., 1993).

Field data sampling and laboratory procedures

Field data sampling was conducted seven times, once in each season, between 2010 (spring, summer and autumn) and 2011 (winter, spring, summer and autumn). For the aboveground biomass, three replicates (size= 0.3 x 0.3 m squares) of each salt marsh plant species were randomly selected in each area and clipped (Caçador *et al.,* 2004). In the laboratory, all samples were washed with ultrapure water (18.2 MΩ cm). The aboveground tissues were then dried at 60 °C until a constant weight was achieved, and the dried tissues were pulverised with a grinding ball mill (Glen Creston MM2000) (Gross *et al*., 1991). Total carbon content was determined using a CHNS/O analyser (Fisons Instruments Model EA 1108). The carbon pool (grams) for each species and for each season analysed was calculated by multiplying the results from the CHNS/O analyser, expressed as a percentage (%), by the biomass according to equation 1.

(Eq.1)

Sedimentation rates were measured using lengths of wood with millimetre marks, which were buried up to the zero mark level in the area occupied by each species. This procedure was performed in February 2011 in the sampling areas corresponding to the three salt marsh plants. One year later (February 2012), the wooden markers were checked to measure the level corresponding to sediment accumulation in each of the three sampling areas.
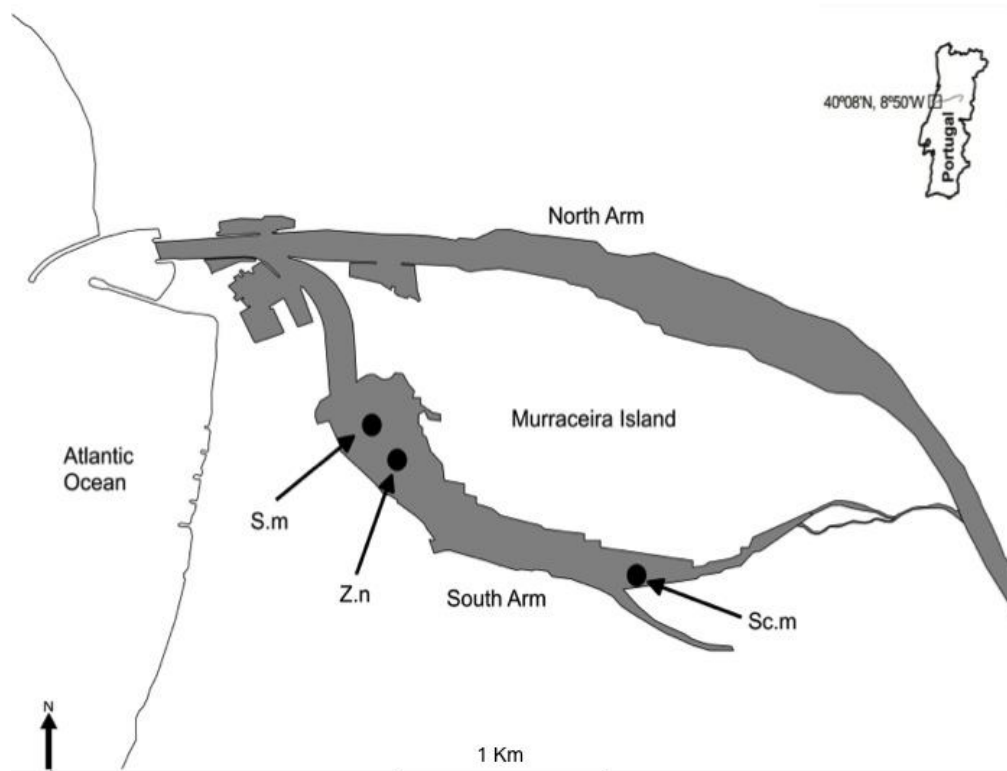

Figure 1. *Sampling locations in the south arm of the Mondego estuary. S.m (Spartina maritima), Z.n (Zostera noltei) and Sc.m (Scirpus maritimus).*

Model

To simulate the growth of a primary producer, a model must include the principal physiological processes, such as photosynthesis, respiration and exudation (Duarte, 2011). The present study follows the work of Simas *et al.* (2001), where fluxes are expressed as gC dry weight m^{-2}; the key equation is

$$\frac{dB}{dt} = \mu - R - L_m - E \tag{Eq.2}$$

where B is plant biomass, μ is gross productivity, R is respiration, L_m is leaf mortality and E is exudation. Gross production (μ) is represented by equation 3:

$$\mu = P_{max} \times f(T) \times f(I) \times f(N) \tag{Eq.3}$$

where P_{max} is the plant's maximum production, $f(T)$ is the air temperature function, $f(I)$ is the light function and $f(N)$ is the nutrient function.

P_{max} values for each studied plant species are shown in table I. The air temperature function $f(T)$ is described in equation 4 (Bach, 1993):

$$f(T) = \gamma_1^{(T-T_{opt})} \tag{Eq.4}$$

where γ_1 is the temperature coefficient for growth, T is the daily air temperature and T_{opt} is the optimum temperature for growth.

The daily temperature variation (T) throughout the year was obtained from a modified sine equation (Anastácio *et al.*, 1995) (Equation 5):

$$T = \frac{(T_{max} + T_{min})}{2} + \frac{(T_{max} - T_{min})}{2} \times SIN\left(\left(\frac{time}{365} - 0.23\right) \times 2 \times \pi\right) \tag{Eq.5}$$

where T_{max} is the maximum air temperature (39.2°C) and T_{min} the minimum air temperature (-2.4°C) during the study period. The maximum and minimum temperature values were obtained from the Portuguese Meteorology Institute (IPMA).

The light function was defined as a Michaelis-Menten equation:

$$f(I) = \frac{I}{I_k + I} \tag{Eq.6}$$

where I is the light intensity and I_k is the half-saturation constant. Daily values of light intensity at 40° latitude were obtained from the Portuguese Environment Agency (APA), and half-saturation constants for the three plant species were obtained from the literature (Morris, 1982).

The regulation of growth by nitrogen ($f(N)$) is expressed in Equation 7:

$$f(N) = \frac{N}{(N+\eta)} \qquad \text{(Eq.7)}$$

where N is the concentration (%) of nitrogen in the leaves and η is the half-saturation constant (%) for nitrogen.

Leaf mortality (L_m) is dependent on temperature (equation 8):

$$L_m = L_{max} \left(\gamma_2^{T-T_{opt}} \right) H \qquad \text{(Eq.8)}$$

$L_m = L_{max} \left(\gamma_2^{T-T_{opt}} \right)$ where L_{max} is the maximum leaf mortality rate, γ_2 is the temperature coefficient for leaf mortality and H is the loss of aboveground biomass due to wave motion, calculated using equation 9:

$$H = 1 + W_1 e^{-W_2 h} \qquad \text{(Eq.9)}$$

where W_1 and W_2 are constants and h is the tidal height.

Exudation (E) (equation 10) is the release of dissolved organic carbon and can be calculated as a fraction of gross production (Baretta-Bekker *et al*. 1997):

$$E = \mu[\alpha + (1 - \alpha)(1 - f(N))] \qquad \text{(Eq.10)}$$

where α is the fraction of gross production that is excreted under nutrient stress conditions (Simas *et al*. 2001).

The respiration rate (R) is dependent on the temperature and on the assimilated biomass (Baretta-Bekker *et al*., 1997) and can be calculated as in equation 11:

$$R = r^{bas} Q_{10}^{T/(T_{opt}-1)} + q^{res} (\mu - E) \qquad \text{(Eq.11)}$$

where r^{bas} is the basal respiration, Q_{10} is the Q_{10} value and q^{res} is the fraction of production lost by respiration.

Model calibration and scenario simulations

The model was built using STELLA software (version 9.0) (Isee systems). As in Simas *et al*. 2001, the model was calibrated independently for C_3 (*Scirpus maritimus*) and C_4 (*Spartina maritima*, *Zostera noltei*) species. The model was run for a two-year period corresponding to the sampling period, and the predictions were compared with the observations. The parameter values used in the model are shown in table I.

To test the influence of temperature on the biomass production of the three plant species in the model, the temperature was increased by 1.5 °C.

Sensitivity analyses

A sensitivity analysis was performed on selected key parameters to assess the variation in the biomass of the three salt marsh plants when the parameters were changed. The parameters were changed in ±10% steps (Jørgensen and Fath, 2011).

Sea level increase

To study the sedimentation rate associated with the area occupied by each studied salt marsh species relative to sea level increase, the bathymetry of the area occupied by each plant was considered along with the average height of each plant species, namely, 1.20 m for *S. maritimus*, 0.7 m for *S. maritima* and 0.3 m for *Z. noltei*. A sea level increase of 0.97 cm per year was simulated and compared with the sedimentation rate of each species. Bathymetry data for the Mondego estuary were extracted from Kenov *et al.* (2012), and the average maximum and minimum tidal heights were obtained from the Portuguese Hydrographic Institute (IH). A constant sedimentation rate (2.7 cm y^{-1} for *Z. noltei*, 1 cm y^{-1} for *S. maritima* and 0.2 cm y^{-1} for *S. maritimus*) and constant rate of sea level increase (0.97 cm y^{-1}) were assumed.

Statistical analysis

To compare the biomass results between the model simulation using the actual temperature and the simulation with the 1.5 °C increase in temperature, a one-way ANOSIM test using Primer software, version 6 (Clarke, 1993) was performed. The model predictions and observations were compared using a regression analysis.

***Table 1**. Parameters values used in the model. A major part of the values were gathered from the works of Simas et al. 2001 and 2007.*

Code	Description	Units	*Scirpus maritimus*	*Spartina maritima*	*Zostera noltei*	References
P_{max}	Maximum production rate	gC dw m^{-2} d^{-1}	1.23	2.4	0.27	Curtis *et al.*, 1989a; Curtis *et al.*, 1989b; Sousa *et al.*, 2010; Bach, 1993
γ_1	Temperature coefficient for growth	-	1.1	1.08	1.08	Bach 1993
T_{opt}	Optimum temperature for growth	°C	21	25	25	Giurgevich and Dunn 1981
I_k	Light half saturation constant	W m^{-2}	177	250	250	Morris 1982
η	Nitrogen half saturation constant	%	0.36	0.36	0.36	Morris 1982
L_{max}	Maximum leaf mortality rate	gC dw d^{-1}	0.812	0.5774	0.0641	*
γ_2	Temperature coefficient for leaf mortality	-	1.07	1.07	1.07	Bach 1993
W_1	Coefficient for H (Eq. 8)	-	30	30	30	Bach 1993
W_2	Coefficient for H (Eq. 8)	m^{-1}	1.5	1.5	1.5	Bach 1993
α	Exudation under nutrient stress	-	0.2	0.2	0.2	Bach 1993
r^{bas}	Basal respiration	d^{-1}	8.4 x 10^{-4}	5.52 x 10^{-4}	5.52 x 10^{-4}	Simas et al. 2001
Q_{10}	Q$_{10}$ value	-	2	2	2	Baretta-Bekker et al. 1997
q^{res}	Production respired fraction	-	0.1	0.1	0.1	Baretta-Bekker et al. 1997

* Values estimated at calibration.

Results and discussion

Model predictions and observed biomass

The model results followed the same pattern as the observed values (Fig. 2), with plant aboveground biomass values usually higher in the warm seasons than in the cold seasons, as also shown by several other studies (Caçador *et al.*, 2004; Couto *et al.,* 2013; Duarte *et al.* 2012; Lillebø *et al.,* 2003). Because the observed values in the spring of 2010 for *S. maritimus* and *Z. noltei* were unusually high, they were excluded from the linear regression calculations. The regression (Fig. 2) demonstrated that the observed and model results showed similar variation, although the data for *S. maritima* showed the best fit, followed by *S. maritimus* and *Z. noltei*. The sensitivity analysis (table II) showed that the parameters with the greatest influence on the biomass values of the three plant species were the maximum temperature (T_{max}) and the maximum leaf mortality rate (L_{max}). A change of ±10% in these parameters could increase or decrease the average biomass by more than 50%.
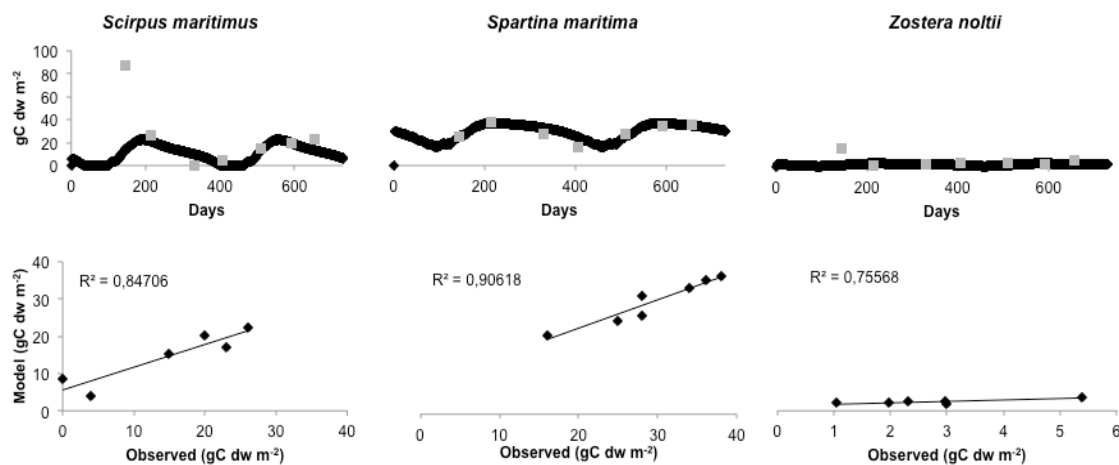

Figure 2. *Observed (grey squares) and model (black line) values during 730 days and linear regression comparing both results for each species.*

Temperature increase

IPCC reports (IPCC, 2007) state that the global temperature has increased approximately 0.3 °C every 10 years since 1979. Fig. 3 shows the results of a comparison between the model results with the actual temperature and the model results assuming an increase of 1.5 °C. The results indicate that in such a scenario (a temperature increase of 1.5 °C), *S. maritimus* and *Z. noltei* would show an increase of approximately 30% in maximum biomass compared with the simulation using the actual temperature, whereas *S. maritima* would show an increase of 10% in maximum biomass.

The increase in temperature apparently has a positive effect in the model, as the increased plant biomass promoted by the increased temperature will absorb more carbon from the atmosphere. However, temperature increase will certainly affect the system in other ways. For example, it will cause sea level to increase due to oceanic thermal expansion, and also due to the melting of Arctic and Antarctic ice (Titus *et al.*, 1991). This process could be detrimental to salt marshes because the sea level increase would place increased stress on certain marshes; these marshes might ultimately be submerged (Silliman *et al.*, 2009).

Table 2.. *Sensitivity analyses of the average biomass of the total study period in relation to key parameters. The results are in percentage of the standard model. Sc.m: S. maritimus; S.m: S. maritima; Z.n: Z. noltei.*

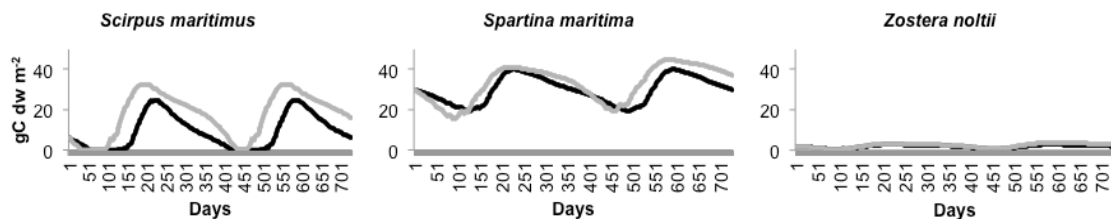| Parameters	Sc.m		S.m		Z.n	
	10%	-10%	10%	-10%	10%	-10%
I_k	-40	52	-37	40	-49	76
T_{max}	322	-83	43	-30	79	-44
T_{min}	0,2	-0,1	-4	1	-1	0
N	41	-41	23	-30	44	-40
η	-38	46	-27	27	-37	49
r^{bas}	-0,3	-0,3	-4	-4	-3	2
Q_{10}	-0,4	-0,3	-4	-4	-3	2
q^{res}	-14	14	-10	6	-17	16
L_{max}	-72	187	-70	80	-76	145

Figure 3. *Model results for the actual temperature (black line) and for the 1.5 °C increase in the temperature (grey line) during 730 days.*

Sea level increase and sedimentation

Kenov *et al*. (2012) have shown that the bathymetry data of the sand banks for the three studied species in the Mondego estuary correspond to an elevation of approximately 2 m above sea level. The average heights of the studied species are 1.20 m for *S. maritimus*, 0.7 m for *S. maritima* and 0.3 m for *Z. noltei*. The sum of the heights of the banks and the average height of each species is approximately 3.2 m for *S. maritimus*, 2.7 m for *S. maritima* and 2.3 m for *Z. noltei*. In 2011, the average low tide was 0.9 m, and the average high tide was 3 m. *Z. noltei* had the highest sedimentation rate for a one-year period (2.7 cm y^{-1} ± 0.2), followed by *S. maritima* with 1 cm y^{-1} ± 0.1 and *S. maritimus* with the lowest sedimentation rate (0.2 cm y^{-1} ± 0.04). Along western European coasts, the sea level has been increasing at least since the Roman Period, and this increase has accelerated during the Modern Period (Pye, 1995). Salt marshes can keep pace with the sea level increase, but this ability depends on the sedimentation rate (Reed *et al.,* 1990; Pont *et al*., 2002). In this case, *S. maritimus* could be at risk in the Mondego estuary. Fig. 4 shows that in approximately 37 years, if the sedimentation rates and rates of sea level increase remain the same (which is unlikely), the *Z. noltei* area would not be immersed during a high tide. As a result, this species would, most likely, disappear from this area. The *S. maritima*

sedimentation rate (1 cm y^{-1}) and sea level (0.9 cm y^{-1}) are increasing to a similar extent, and the *S. maritima* area should not be greatly influenced by the increasing sea level during the next 50 years. Unlike *Z. noltei*, *S. maritimus* could be completely covered during every high tide in approximately 40 years. Of the three study species, *S. maritimus* should show the greatest effects of the sea level increase because its sedimentation rate (0.2 cm y^{-1}) is lower than the expected rate of increase of sea level. Before the *S. maritimus* area becomes completely submerged, this species will, most likely, be influenced by the salinity increase that accompanies an increase in sea level. Lillebø *et al.* (2003), working with *S. maritimus* in the same area, showed that salinity affects the dynamics of *S. maritimus*. In fact, the findings of previous studies have indicated that lower biomass values are associated with high salinity, showing that the survival of this species could be threatened by high salinity. Couto *et al.* (2013) showed that *S. maritimus* accumulated approximately 21 tons of carbon in the tissues in 21 months, compared with 1.9 tons of carbon accumulated in the tissues by *S. maritima* and 0.9 ton by *Z. noltei*. If the species that accumulates the highest amount of carbon of the three species disappears, the carbon sequestration ability of the Mondego estuary may decrease. Silliman *et al.*, 2009 suggest that as much as 90% of tidal marshland worldwide could be in jeopardy by 2100 because of the increase in sea level.
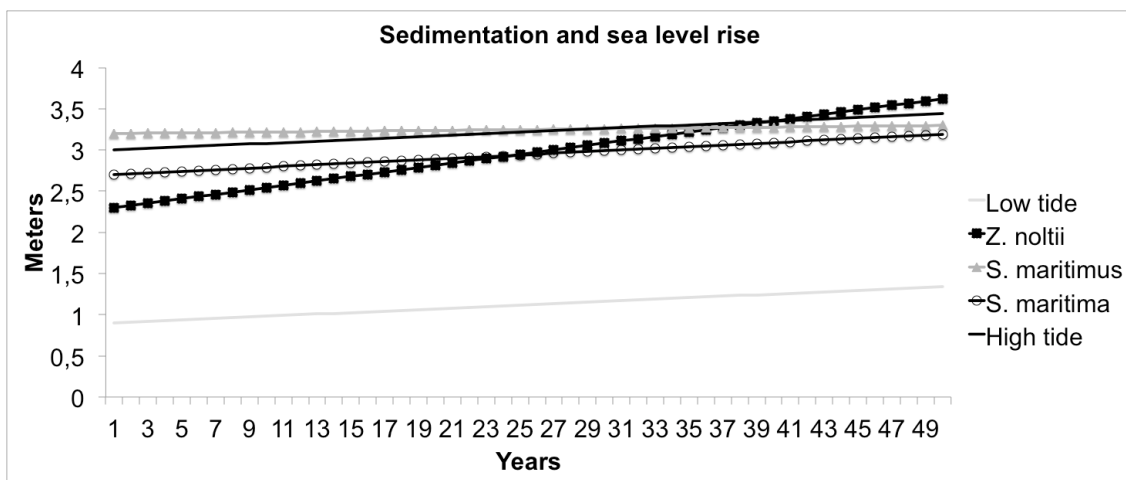

Figure 4. Predicted sea-level rise and sedimentation of the three studied species through 50 years

Conclusions

The fit of the models for the C$_3$ and C$_4$ plants to the observed biomass values was highly satisfactory. The assumption of a temperature higher than the actual temperature yielded simulated plant biomass values higher than the actual values. This result indicates that the biomass of both C$_4$ and C$_3$ plants would increase and that as a result, carbon sequestration would also increase. The increase in sea level should be prejudicial to salt marsh species. The *S. maritima* sedimentation rate can apparently keep pace with the sea level increase, and *Z. noltei* shows a high sedimentation rate. In contrast, because the *S. maritimus* sedimentation rate is very low, this species could disappear from the Mondego estuary. This scenario would have important implications for the system's carbon sequestration ability because, of the three species examined, *S. maritimus* accumulates the highest quantity of carbon.

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