

Nutrient enrichment and the role of salt marshes in the Tagus estuary (Portugal)

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Abstract

Eutrophication is one of the most common impacts of nutrient enrichment on coastal ecosystems. Since there is a wide ecosystem response variety in scale, intensity and impact to nutrient enrichment, the loading required to produce eutrophication symptoms to each system is also variable. In estuaries and coastal zones salt marsh primary producers have received less attention, mainly because salt marsh dominated systems are considered less sensitive to nutrient enrichment and, for that reason, their response is slower and more difficult to quantify. Salt marshes have been considered as major attenuators of the effects of nitrogen enrichment in several coastal systems, and are indicated as a measure of the system susceptibility to nutrient enrichment. The main goal of the present work is to discuss the role of salt marsh vegetation in the nutrient dynamics of coastal systems and in the nutrient enrichment process. For these purposes salt marsh vegetation growth in the Tagus estuary is described through a mathematical model which includes the simulation of the nutrient dynamics through the sediment–water interface and the uptake kinetics by the vascular plants. An analysis of the role of salt marsh vegetation on the nutrient dynamics of the Tagus estuary is carried out through the discussion of the model results and comparison with data obtained for other primary producers in the system. The results indicate that C_4 salt marsh plants have the highest productivity, followed by seaweeds. The total net production of salt marsh plants and is about 12,600 ton C yr⁻¹, accounting for 25% of the total primary production within the system.

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1. Introduction

In estuaries and coastal zones, the most vulnerable or sensitive primary producers to nutrient enrichment are generally those directly dependent on water quality, which are usually examined in current eutrophication assessment methods: phytoplankton, macroalgae and submerged aquatic vegetation (here defined as vascular plants). Other primary producers such as salt marsh vegetation have received less attention, mainly because salt marsh dominated systems are considered less sensitive to nutrient enrichment and, for that reason, their response is slower and more difficult to quantify. In general,

all wetland systems are known as very productive environments acting as water filters and thus contributing to water quality improvement (Mitsch and Gosselink, 2000). Studies conducted by Teal (1962) in Sapelo Island led to the formulation of the “outwelling hypothesis” (Nixon, 1980; Odum, 1980), which postulates that salt marshes are exporters of organic matter (energy) to the coastal zone, providing food resources which support marine productivity in coastal systems. However, other studies show opposite results, concluding that salt marshes act as organic matter and nutrient sinks (Nixon, 1980; Dankers et al., 1984; Whiting et al., 1989; Dame et al., 1991). These results show that the outwelling hypothesis may not be generally applied (Nixon, 1980; Bettencourt et al., 1994).

It has been assumed that in pristine conditions salt marshes are in equilibrium as sources or sinks of different forms of nitrogen between salt marsh and seawater (Valiela and Teal,

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1979a,b). Furthermore, over the long term there is a flux balance in the marsh which means that, e.g. a marsh can be a sink for particulate organic forms and a source of dissolved organic ones (Wolaver and Spurrier, 1988). However, in hypereutrophic conditions, salt marsh sediments have the capacity to become sinks, particularly for nitrate, as benthic denitrification responds to elevated nitrate concentrations and acts as a nitrogen buffer (King and Nedwell, 1987; Koch et al., 1992; Nedwell, 2000). However, salt marshes will only act as sinks for nitrogen if nitrate removal by denitrification exceeds the tidal export of other forms of nitrogen, including ammonium, and dissolved and particulate organic nitrogen (Valiela and Teal, 1979a,b).

One response to the nitrogen increase in salt marsh sediments is increased productivity of vascular vegetation species and increased standing stocks, followed by increased rates of vegetation decay, at least initially, and by higher community respiration rates (Mitsch and Gosselink, 2000). Changes in species composition are an additional response to eutrophication (Craft et al., 1995; Vaithyanathan and Richardson, 1997). Furthermore, an increase in productivity of salt marsh vegetation due to nutrient enrichment (particularly nitrogen) can be responsible for the more oxidized conditions of the sediments beneath (Howes et al., 1981) through the rise of oxygen released from the roots into the anoxic sediments (an adaptation of the root system to the nitrogen uptake in anoxic conditions). This process reduces the ability of salt marsh sediments to retain metals through the decrease of metal sulphide precipitation (Giblin et al., 1986). The increase of available heavy metal forms in the sediments can also affect vascular vegetation due to its ability for heavy metal bioaccumulation, although the physiological impact of this process is not well studied (Padinha et al., 2000).

The description of the structure and function of the salt marsh ecosystem through modelling has been developed in several conceptual and mathematical models (e.g. Wiegert et al., 1981; Morris, 1982; Chalmers et al., 1985; Morris and Bowden, 1986; Wiegert, 1986) focusing on the comprehensive study of nutrient budget and dynamics. Such models include vascular vegetation as a major compartment and its production is often simulated for above and belowground plant parts. The inclusion of the belowground growth simulation is important not only because the biomass of roots and rhizomes generally exceeds the aboveground biomass, but also because of its particular role in the nutrient uptake, which influences the overall plant growth dynamics. In fertilization experiments, a reduction in the roots and rhizomes, together with an increase in the aboveground vegetation, was observed when nutrient doses were highest (Valiela et al., 1976). The authors conclude that “the grasses seemed to manufacture enough roots to process needed nitrogen and no more” and that “the amount of roots is inversely proportional to the available nitrogen in the sediment”. In the model developed by Morris and Bowden (1986) for an Atlantic coast salt marsh, calculations of N and P export were sensitive to small changes in belowground production. It was also demonstrated by this model that the recycling of nutrients is higher for mature marshes with deep sediments than for younger marshes.

Nitrogen is usually the limiting nutrient to salt marsh vegetation production (Mendelssohn, 1979) and its availability is shown to increase productivity, e.g. transforming the morphology of species such as the dwarf form of *Spartina alterniflora* into the tall form (Valiela and Teal, 1974; Valiela et al., 1978). The nitrogen uptake rate of salt marsh species such as *Spartina* is higher for ammonium (Morris, 1980). Nitrate plays a minor role in the plant nitrogen nutrition, although when it is made available the plants have shown the capacity for its assimilation (Mendelssohn, 1979). The description of salt marshes as efficient sinks for ammonium (Wolaver et al., 1983) and the high pore water concentrations in some marsh soils (Mendelssohn, 1979) seem to be inconsistent with the nitrogen-limited condition of the salt marsh plants. However, studies on the nitrogen uptake kinetics of *S. alterniflora* indicate that its nitrogen-limited condition seems to be dependent not only on the availability of nitrogen species but also on a group of edaphic conditions such as oxygen deficiency, sulphide toxicity and salinity (Bradley and Morris, 1990). Since the marsh sediments are generally anoxic, it is well established that an adequate supply of oxygen to the root system optimises the ion uptake rates (Engelaar et al., 1993). This process is supported by the ability of the plant to internally supply oxygen to the roots and depends on the anoxic level of the marsh soil (water-logging conditions), since the plant does not conduct sufficient oxygen to the roots in highly reduced substrates (Mendelssohn et al., 1981). The limitation or inhibition of nitrogen uptake is also possible when hydrogen sulphide is present in high quantities (Ornes and Kaplan, 1989; Bradley and Morris, 1990). High salinities are also responsible for the decrease in the plant nutrient uptake, due to the competition for binding sites on the carriers (Morris, 1980). An empirical model of nitrogen uptake kinetics of *S. alterniflora* was presented by Morris (1980) based on Michaelis–Menten equations expressed as exponential functions of temperature. The model was adjusted separately for the uptake rates of ammonium and nitrate observed in laboratory cultures.

Several processes that take place in aerobic and anaerobic layers influence the availability of ammonium within the sediments. Ammonium is produced by diagenesis (decay of particulate organic nitrogen) in both layers but the production is smaller in the narrow (1–2 mm) the aerobic layer. Nitrification is restricted to the aerobic layer. The ammonium loss from the sediments occurs by diffusion between adjacent layers, including the water column, and sedimentation (DiToro, 2001). Several models have been proposed for the distribution of ammonium in pore water considering these processes (e.g. Billen et al., 1989; Klump and Martens, 1989; Blackburn, 1990; DiToro et al., 1990).

Salt marsh systems have been considered as major attenuators of the effects of nitrogen enrichment in several coastal systems, and are indicated as a measure of the system susceptibility to nutrient enrichment (NCR, 2000; Nedwell, 2000). However, little has been discussed about how salt marshes may potentially modify the impacts of nutrient enrichment on coastal systems. Recently, the use of wetlands in the evaluation of the ecological quality of European estuarine and coastal waters has

received substantial attention, especially as part of the management requisites for the implementation of the Water Framework Directive (2000/60/EC). Under this Directive these ecosystems are referred as playing an important role in the achievement of the environmental objectives (CIS, 2003).

In this paper the role of salt marsh vegetation on the nutrient dynamics of primary production in the Tagus estuary is discussed. A previous growth model for aboveground salt marsh vegetation growth (Simas et al., 2001) was extended to the simulation of the belowground component of the C₃ and C₄ photosynthetic plants. A module for the ammonium supply to the sediments for plant uptake was also developed. The extended version of the salt marsh and sediment model was integrated in an ecological model (EcoWin2000, Ferreira, 1995) previously developed for the Tagus estuary. GIS tools and field data information collected for C₃ and C₄ species in the Tagus salt marsh were used to set up and calibrate the model.

2. Methodology

2.1. Model concept and implementation

The general model of an individual shoot was integrated into a detailed ecological model (EcoWin2000) which simulates physical exchanges, biogeochemical processes within the system and population dynamics of the target species (Nunes et al., 2003). Light, temperature, nutrients in the water (used to simulate nutrient dynamics in the sediment) and tides are forcing functions of the model, which were linked to the individual shoot model. The spatial modelling domain is the total estuarine area of the Tagus.

2.1.1. Forcing functions

The light climate in the Tagus was simulated following Brock (1981). Hourly air temperature was modelled by an empirical relationship fitted to measured data over an annual cycle. The dissolved nutrients (NH₄⁺, NO₂⁻ and NO₃⁻) in each box were simulated through the transport (advection–diffusion) object, which acts to redistribute the mass among the boxes rather than to modify this within a box due to the internal processes (through the interaction of “biologically active” objects). The mass of nutrient (ammonium) to the system is simulated through constant loads from point sources to specific model boxes (Ferreira, 1995). The transport of nutrients is forced by tidal exchange, with tidal height being generated from harmonic equations using the Oceanus 2000™ software (Ferreira, 2006).

2.1.2. State variables

2.1.2.1. Salt marsh plant models. Table 1 presents the main equations of the model. For the aboveground parts (stems and leaves), Eq. (1) was used to simulate individual shoot biomass variation. The potential plant production is calculated using light (Eq. (2)) and air temperature (Eq. (3)) functions. The nutrient limitation function is based on an adapted cell-quota

model (Solidoro et al., 1997a,b), which simulates the uptake kinetics as a function of the cell nutrient content (Droop, 1970; Lehman et al., 1975; Baretta-Bekker et al., 1997). The intracellular nutrient status is defined by Eq. (4).

Since ammonium is considered the preferential nitrogen species for salt marsh plant growth (Morris, 1980), the uptake was simulated for this chemical species, which depends on the level of nitrogen concentration in the tissues (Fugita, 1985; Solidoro

Table 1

Generic model equations used for the simulation of the individual C₃ and C₄ plant growth

Model equations	Description
$\frac{dB_{\text{above}}}{dt} = [P_{\text{max}}f(I)f(T)Q] - L_{\text{m}} - r_{\text{above}} - R - S - A_{\text{root}} \quad (1)$	Simulation of aboveground biomass variation
B_{above}	Aboveground biomass
P_{max}	Plant maximum gross photosynthetic rate
r_{above}	Aboveground respiration rate
R	Reproduction rate
A_{root}	Biomass allocation rate from the aboveground to the roots
$f(I) = \frac{I}{(I_k + I)} \quad (2)$	Light function
I	Light intensity
I_k	Half saturation constant for light
$f(T) = \theta_1^{(T-T_{\text{opt}})} \quad (3)$	Air temperature function
T	Air temperature
T_{opt}	Optimum temperature for growth
θ_1	Temperature coefficient for growth
$Q = V \frac{Q_{\text{max}} - Q}{Q_{\text{max}} - Q_{\text{min}}} - P_{\text{max}} \frac{Q - Q_{\text{min}}}{Q - k_c} \quad (4)$	Nutrient cell-quota model
Q	Concentration of the nutrient in the cell
Q_{min}	Nutrient concentration of the structural parts of the cell
Q_{max}	Maximum cell nutrient concentration
k_c	Critical nutrient concentration constant
$V = V_{\text{max}} \frac{N}{N + k_N} \quad (5)$	Uptake rate of ammonium
N	Ammonium concentration in sediment pore water
k_N	Half saturation constant for ammonium uptake
$V_{\text{max}} = a(e^{Tb} - 1) \quad (6)$	Maximum uptake rate for ammonium
a, b	Empirical coefficients
$L_{\text{m}} = L_{\text{max}} \left(\theta_2^{T-T_{\text{opt}}} \right) H \quad (7)$	Leaf mortality
L_{max}	Maximum leaf mortality rate
θ_2	Temperature coefficient for leaf mortality
X_P^R	Critical P/C ratio
$S = \omega L_{\text{m}} \quad (8)$	Senescence
ω	Senescence rate
$\frac{dB_{\text{below}}}{dt} = A_{\text{root}} + S - r_{\text{below}} \quad (9)$	Simulation of belowground biomass variation
B_{below}	Belowground biomass
r_{below}	Belowground respiration rate

et al., 1997a,b). The simulation of the ammonium uptake rate is given in Eq. (5), considering the dependence on a maximum uptake rate (Eq. (6)), an external nitrogen concentration and a saturation threshold (Morris, 1980; Le Bot et al., 1998).

Leaf mortality, respiration, reproduction, senescence and biomass allocation to the roots are sink terms in the plant aboveground production. Leaf mortality is also a temperature-dependent function (Eq. (7)). The action of the tides and wave motion on leaf breakage is simulated through the loss of aboveground biomass which increases with decreasing water height, expressing the greater effect of wave impact in shallower waters. Respiration is simulated as a constant rate and individual shoot reproduction as a biomass investment in vegetative propagation (sexual reproduction is simulated through the population model). Nutrient resorption from senescent leaves (Cartaxana and Catarino, 2002) is simulated through a biomass gain allocated into the root material as a fraction of leaf mortality (Eq. (8)). Belowground growth is simulated as a fraction of the aboveground production allocated into the roots plus the biomass allocation corresponding to nutrient resorption during leaf senescence. Respiratory loss is the sink term in the root growth simulation (Eq. (9)).

Population dynamics was simulated through a class transition model (Press et al., 1995; Ferreira et al., 1998). This sub-model simulates the transition of the shoots between weight classes in order to describe plant population density per unit area. Class transition is expressed by:

$$\frac{\partial n(s,t)}{\partial t} = -\frac{\partial[n(s,t)g(s,t)]}{\partial s} - \mu[(s)n(s,t)] \tag{10}$$

where t , time; s , weight class; n , number of shoots; g , scope for growth (growth rate); μ , mortality rate. The number of shoots in each weight class depends on the individual shoot scope for growth and on an allometric natural mortality rate. Additionally, erosion losses in the number of shoots are higher for lower weight classes, i.e. physical resistance is also simulated allometrically. In the case of salt marsh vegetation four weight classes were established, each one representing a stage in the plant life cycle: weight class 1, young shoots; weight classes 2 and 3, intermediate stages of the shoot life cycle between young and adult stages; weight class 4, adults with reproductive capacity. Recruitment to class 1 is explicitly modelled as a source of new recruits to the population. This is due to the reproduction in weight class 4, and decreases individual shoot scope for growth in this weight class during the reproductive period.

2.1.2.2. *Sediment ammonium model.* The ammonium concentration in the pore water of the sediments is simulated according to DiToro (2001) by solving the mass-balance equation:

$$H \frac{d[\text{NH}_4(\text{sed})]}{dt} = k_{\text{PON}}H[\text{PON}] + K_{\text{Lws}}([\text{NH}_4(\text{wat})] - [\text{NH}_4(\text{sed})]) - w_{\text{NH}_4}[\text{NH}_4(\text{sed})] \tag{11}$$

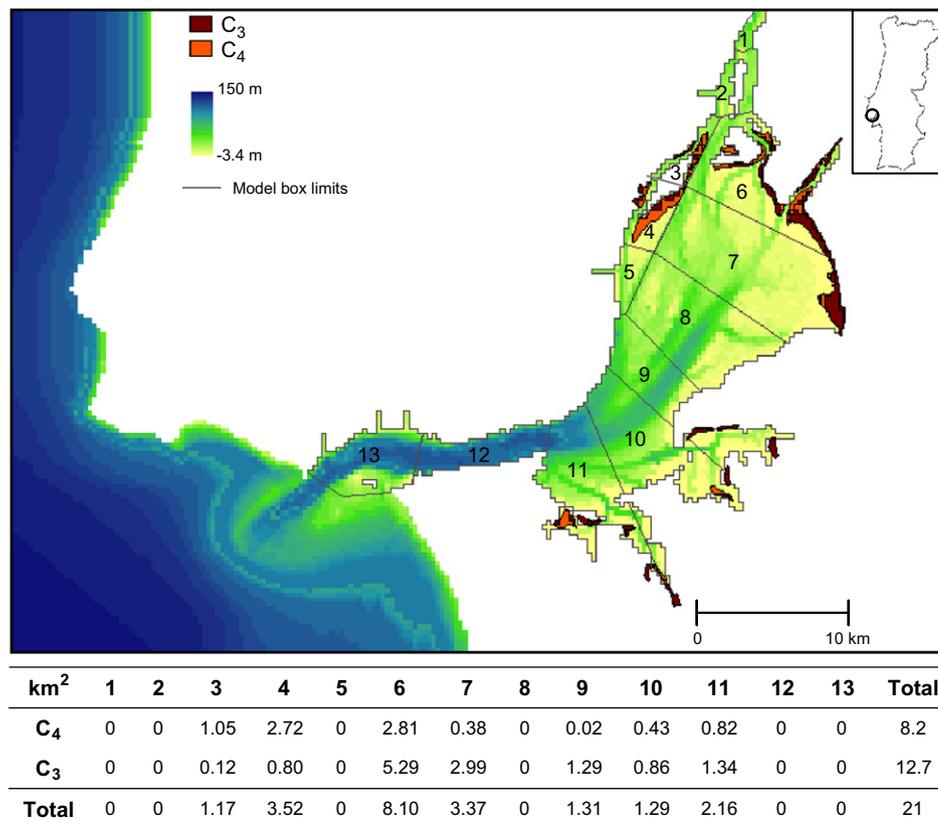


Fig. 1. Model box limits, distribution of C₃ and C₄ vegetation according to the Corine Land Cover 2000 information (EEA, 2005) and resulted areas per box calculated with GIS tools.

where [PON] is the particulate organic nitrogen (mg N m^{-3}); k_{PON} is the decay rate of PON to ammonium (d^{-1}); H is the sediment height (m); K_{Lws} is the diffusion coefficient of ammonium (m d^{-1}); $[\text{NH}_4(\text{sed})]$ is the ammonium concentration in the sediment (mg N m^{-3}); $[\text{NH}_4(\text{wat})]$ is the ammonium concentration in the overlying water (mg N m^{-3}); and w_{NH_4} is the ammonium loss rate via sedimentation (m d^{-1}). The variation of PON in the sediment layer is simulated through the losses via mineralisation (the first right hand term of Eq. (11); DiToro, 2001):

$$H \frac{d[\text{PON}]}{dt} = J_{\text{PON}} - k_{\text{PON}}H[\text{PON}] - w_{\text{PON}}[\text{PON}] \quad (12)$$

where J_{PON} is the flux of PON to the sediment ($\text{mg N m}^{-2} \text{d}^{-1}$) and w_{PON} is the loss of PON via sedimentation (buried in the sediment) (m d^{-1}). The flux of PON to the sediment is calculated through the simulation of suspended particulate matter variation in the water and the average value of PON calculated from observed data in the Tagus estuary.

2.2. Model architecture and operation

In order to link the simulation of the system physical processes, the individual and population models were ported to EcoWin2000 (Ferreira, 1995) an object-oriented modelling platform. The objects of the model encapsulate the forcing functions and state variables; these can be switched on and off in order to test the sensitivity of the different compartments in the model. Object properties can be inherited by the descendants, making it possible to establish object hierarchies and improve code reusability and security. A detailed ecological model can be developed for any system, which includes physical exchanges with the ocean boundary, biogeochemical processes, and individual and population growth of target species (Nunes et al., 2003; Nobre et al., 2005).

To develop the salt marsh vegetation object the existing objects for simulation of the water flow, hydrodynamics (transport), dissolved substances (ammonium), suspended particulate matter (SPM), light, tides and air temperature in the Tagus estuary were used. To simulate the water flow and the transport within the system (advection–diffusion), the system was divided into 13 boxes (Fig. 1), used for spatial

Table 2
Parameters used in the vegetation growth and sediment ammonium models. *Summer value; **winter value; ***value estimated at calibration

	Parameter	Description	Units	C ₄	C ₃	References	
Vegetation growth	P_{max}	Maximum production rate	d^{-1}	0.43	0.08	Morris (1982), Catarino et al. (1985)	
	I_k	Half saturation constant for light	W m^{-2}	250	177	Morris (1982)	
	T_{opt}	Optimum temperature for growth	$^{\circ}\text{C}$	25	21	Giurgevich and Dunn (1981)	
	θ	Temperature coefficient for growth	–	1.08	1.10	Bach (1993)	
	Q_{min}	Nutrient concentration of the structural parts of the cell	mg L^{-1}	0.05		***	
	Q_{max}	Maximum cell nutrient concentration	mg L^{-1}	0.18	0.45	***	
	k_c	Critical nutrient concentration constant	mg L^{-1}	0.01		Solidoro et al. (1997a,b)	
	k_N	Half saturation constant for nutrient species uptake	mg L^{-1}	0.057	0.041	Morris (1980)	
	a	Empirical coefficients for maximum nitrogen uptake	–	0.015	0.026	Morris (1980)	
	b	–	–	0.116	0.041	Morris (1980)	
	L_{max}	Maximum leaf mortality rate	d^{-1}	0.05		***	
	σ	Temperature coefficient for leaf mortality	–	1.07		Bach (1993)	
	W_1	Empirical coefficients for tide on leaf action	–	30		Bach (1993)	
	W_2	–	–	1.5		Bach (1993)	
	R	Reproduction rate	d^{-1}	0.13	0.10	***	
	ω	Senescence rate constant	d^{-1}	0.08*	0.9	Cartaxana and Catarino (1997, 2002)	
		r_{above}	Aboveground respiration rate	d^{-1}	0.04		***
		r_{below}	Belowground respiration rate	d^{-1}	0.015*	0.05*	***
		A_{root}	Biomass allocation rate from the aboveground to the roots	d^{-1}	0.001**	0.001**	***
		S	Number of weight classes	–	0.03		***
	μ	Class mortality rate	d^{-1}	0.0320	0.0024	***	
				0.0080	0.0020		
				0.0012	0.0015		
				0.0009	0.0015		
	M_{root}	Root mortality rate for the population model	d^{-1}	0.5	0.2	***	
NH_4^+ in sediments	k_{Lws}	Diffusion coefficient of ammonium	m d^{-1}	0.00017		Boudreau (1996)	
	k_{PON}	Decay rate of PON to ammonium	d^{-1}	0.03		Cartaxana and Catarino (1997, 2002)	
	w_{NH_4}	Ammonium loss rate via sedimentation	m d^{-1}	0.0007		***	

discrimination. A class for ammonium in sediments was built and coupled to the salt marsh object. Plant growth was simulated considering the individual shoot processes (individual object), which were then inherited by the population class to simulate population dynamics (population object). For each photosynthetic pathway an independent class for the simulation of nutrients was built considering the different areas of C_4 and C_3 colonisation. The growth simulation of both plant photosynthetic pathways was implemented through a “wrapper” object, which manages the two C_4 and C_3 population objects. These are hidden from other objects in the model and managed only by the wrapper, which is exposed to all forcing functions and state variables (Nunes et al., 2003).

2.3. Calibration and validation

Model calibration was done independently for C_3 and C_4 plants using literature data for parameter constants (Table 2). A field dataset collected in the Tagus estuary between April and November 2002 was used to validate shoot (only in the case of C_4 species) and population growth of salt marsh vegetation. For the C_3 simulation two data sets of observed monthly biomass values for *Arthrocnemum fruticosum* and *Halimione portulacoides* were used to calibrate and validate the model. Some parameter values were not found in the literature and, for that reason, were estimated at calibration. The parameters used in the sediment ammonium model are also shown in Table 2. Geographic Information System (GIS) tools, bathymetry data and the Corine Land Cover (EEA, 2005) were used to obtain the salt marsh distribution in the system. The areas occupied by C_3 and C_4 plants were calculated for each model box in order to upscale the model results to the entire system (Fig. 1).

2.4. Sensitivity analysis

A sensitivity analysis was performed to evaluate the effect of variation in key parameter values on the main state variables of the model (plant biomass and ammonium concentration in the sediments). The sensitivity of each variable to a chosen parameter was measured through the fraction (percentage) of the variation in the state variable due to the change in each parameter (adapted from Jørgensen, 1994). The relative change in the parameter values was chosen to be $\pm 10\%$ (Jørgensen, 1994). The corresponding response of each state variable considered is recorded and discussed.

3. Results

3.1. C_4 model – *Spartina maritima*

The comparison of model results with field data for *Spartina maritima* from the lower marsh is shown in Fig. 2. The growing season period predicted for the aboveground biomass starts about one month earlier than in the observed data set. However, the correlation between simulated and observed individual shoot biomass is significant for a 90% confidence

interval. There is a decrease in the simulated individual root biomass during the growing season (from April until August), which is also observed in the field results. A significant correlation (98% confidence interval) between observed and simulated individual root biomass was obtained. The general increase of root biomass during winter months is documented in the literature for *Spartina* species as being induced by the translocation of biomass from the senescing aboveground components (Lana et al., 1991).

The results obtained for the population model are shown in Fig. 3. The predicted distribution of *Spartina* shoots per weight class falls within the observed range of values. Density is higher in the first weight class, and is gradually reduced until the last weight class due to mortality, which is higher in the early life-cycle stages. Maximum values are calculated for summer months in all weight classes. The predicted total density values start to decrease after the maximum obtained for August and fall until April reaching very low values. The model is slightly exceeding the observed density curves particularly for weight class 2, 3 and 4. However, the correlation coefficients between observed and estimated values are significant for all weight classes (Fig. 3).

The observed and predicted biomass values for above and belowground biomass are presented in Fig. 4. Although the model reproduces the observed growing season peak for the aboveground biomass, for the belowground, the single peak obtained by the model only coincides in time with one of the four peaks in

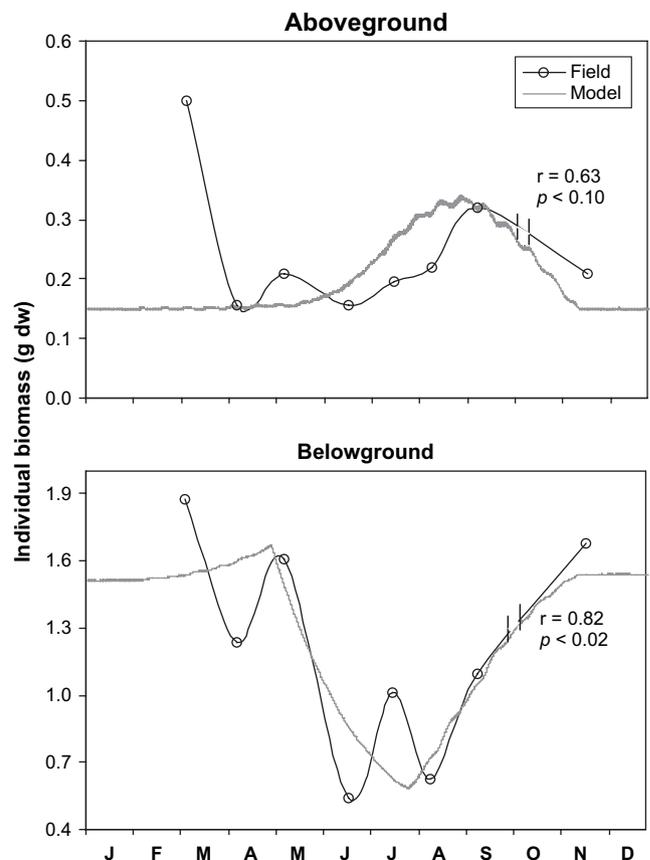


Fig. 2. Field and model results for *Spartina maritima* individual in the Tagus estuary.

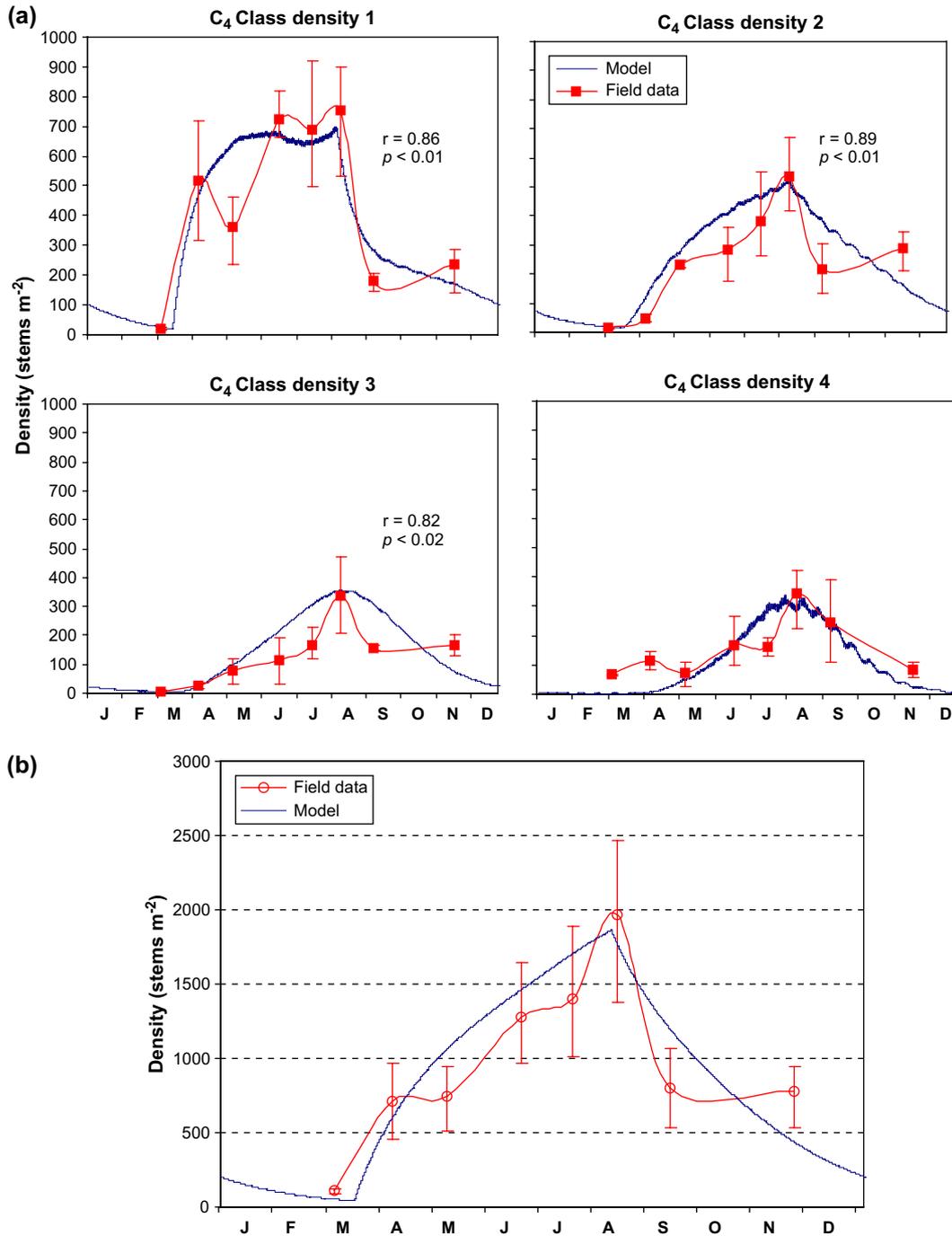


Fig. 3. Observed (mean, maximum and minimum values) and predicted density for the C₄ species *Spartina maritima*: (a) density per weight class; and (b) total density.

the field. However, it should be noted that the observed below-ground biomass distribution is not very solid (with four biomass peaks and a large distance between minimum and maximum estimates), without a defined pattern, which causes some difficulty in model validation. For both above and belowground biomass the estimated values are being slightly overestimated during the growing season and underestimated during the rest of the year particularly for the root system, although due to a lack of observed winter density values the model results could not be validated for this period.

The model estimates a mean net production value of about 3310 g dw m⁻² yr⁻¹. This value is close to the maximum of 3500¹ g dw m⁻² yr⁻¹ estimated at light saturation conditions for *Spartina maritima* in the Tagus salt marsh (Catarino et al., 1985). A much lower value of 670 g dw m⁻² yr⁻¹

¹ Value estimated from the rate 324 mg C m⁻² h⁻¹ (Catarino et al., 1985) using a mean day light period of 12 h and a carbon content of 41% for *Spartina maritima* observed by Cartaxana and Catarino (1997).

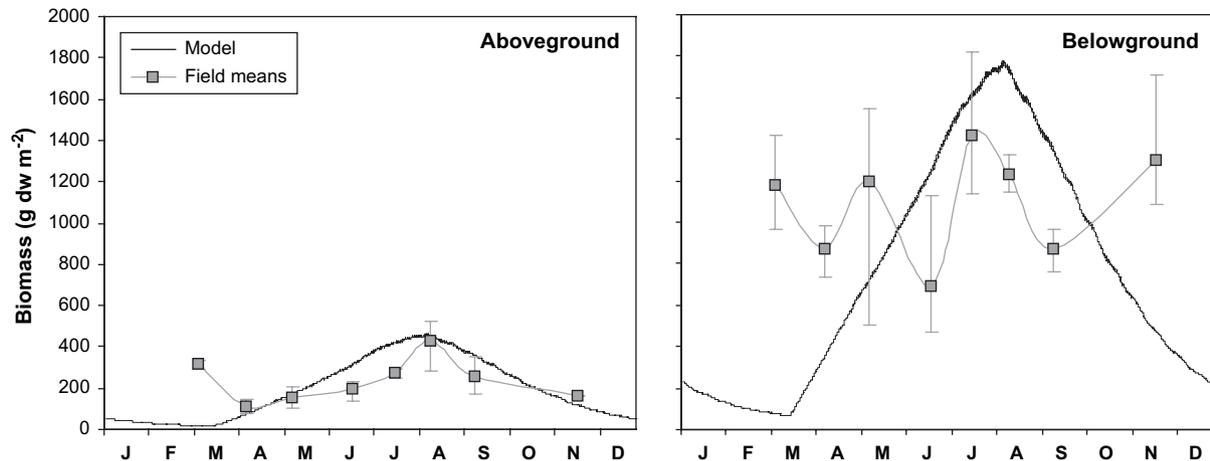


Fig. 4. Observed and predicted biomass values for the C_4 species *Spartina maritima*. Maximum and minimum values for observed results are also presented.

(Catarino, 1981) was also measured through monthly variation of dry weight, which is notoriously error-prone. However, the mean value estimated by the model is within the observed literature range for *Spartina* species. Further field studies of production of the Tagus salt marsh species are needed in order to confirm the model estimates.

3.2. C_3 model – upper and middle salt marsh species

The comparison between the observed and predicted values is presented in Fig. 5. A significant correlation was only obtained for the belowground biomass of *Halimione portulacoides* although the predicted means (1962 g dw m^{-2} for aboveground and 1600 g dw m^{-2} for belowground) fall within the range of observed data ($983\text{--}5527 \text{ g dw m}^{-2}$ for aboveground and $693\text{--}3515 \text{ g dw m}^{-2}$ for belowground). It should be noted that the model mean is annual whilst the observed mean corresponds only to the growing season. If winter biomass values were also included in the observed set the mean value would probably be lower.

The net production calculated by the model for the C_3 salt marsh species is about $516 \text{ g dw m}^{-2} \text{ yr}^{-1}$, which is close to the maximum of $540^2 \text{ g dw m}^{-2} \text{ yr}^{-1}$ estimated for *Arthrocnemum fruticosum* in the Tagus salt marshes (Catarino et al., 1985). These values are also within the reported range for several European C_3 salt marsh species.

3.3. Nutrient dynamics in sediments and water

In sediments without salt marsh plants, the model results for the ammonium concentrations varied from 11 to 30 g N m^{-3} (Fig. 6a). The ammonium concentrations were lower for sediments with salt marsh vegetation, varying from 4 to 13 g N m^{-3} (Fig. 6a). For all sediment types, the ammonium concentrations are higher during winter and decrease

during spring and summer. This pattern is stronger in the sediments colonised by salt marsh plants, with ammonium concentrations showing a higher range of values. The spatial distribution of ammonium concentrations in the sediment shows a decrease towards the estuary mouth (Fig. 6a).

The model results show that the ammonium uptake by salt marsh plant roots reduces the ammonium concentration in the sediment by about 80% in C_4 sediments and about 70% in C_3 sediments (Fig. 6b). There is a seaward increase in the percentage of the ammonium removed by plants as well as a more efficient uptake of the nutrient by the C_4 than the C_3 plants and, for this reason, the ammonium concentrations in C_3 sediments remain higher than those in C_4 sediments during part of the year. The ammonium concentrations in the water are shown to be slightly lower in the boxes with salt marshes (Fig. 7).

The estimated ammonium efflux is higher for the sediments without plants. The mean diffusion rates varied from 9.6×10^{-3} to $2.5 \times 10^{-2} \text{ g N m}^{-2} \text{ h}^{-1}$ in sediments without plants and from 2.1×10^{-3} to $5.7 \times 10^{-3} \text{ g N m}^{-2} \text{ h}^{-1}$ in salt marsh sediments.

The model shows a higher ammonium efflux in the upstream part of the estuary for the largest salt marsh areas and higher ammonium concentrations in the sediments. The ammonium flux to the water column is higher for the C_3 than for the C_4 sediments due to the differences in the ammonium uptake efficiencies referred above. A comparison of the net ammonium diffusion per unit area of the sediment–water interface for the different types of sediment is shown in Fig. 8.

3.4. Sensitivity analysis

The vegetation growth model is most sensitive to the parameters related to leaf mortality and class mortality rates (Table 3). This is particularly evident for the decrease in class mortality rates of the C_4 model. These results can indicate the possible vulnerability of the salt marsh plants to leaf smothering by sediment deposition resulting from the construction of fish aquaculture tanks, which in 2001 destroyed about 17 ha of

² Value estimated from the rate $35 \text{ mg C m}^{-2} \text{ h}^{-1}$ (Catarino et al., 1985) using a mean day light period of 12 h and a carbon content of 29% for *Arthrocnemum fruticosum* observed by Cartaxana and Catarino (1997).

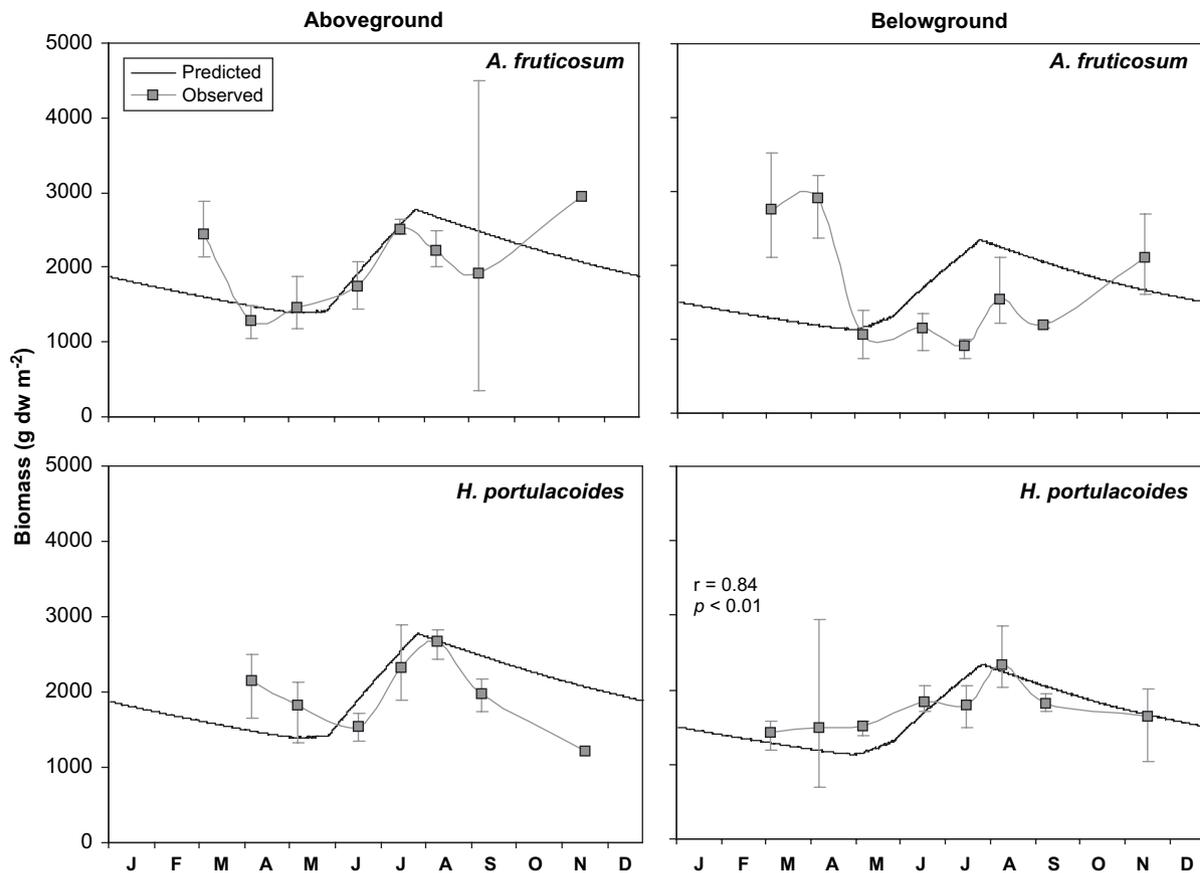


Fig. 5. Observed and predicted biomass values for the main C_3 species. Maximum and minimum values for observed results are also presented.

salt marshes near the sampling site. This intervention could be the cause for the biomass reduction observed between the current field data and the results obtained 20 years ago. Further field and laboratory studies are needed to test the parameters used in the growth model in order to make the model more robust.

For the sensitivity analysis of the sediment ammonium model, the ion concentrations were compared between sediments with and without plants. For this purpose, the results for ammonium in C_4 sediments were used. The ammonium sedimentation is the most sensitive parameter to the ammonium concentrations in the sediment. It is also observed that in C_4 sediments the diffusion of ammonium is made towards the sediment because when this parameter is reduced the ammonium concentration in the sediment decreases. The decay rate of PON to ammonium also affects salt marsh C_4 sediments to a deeper extent due to the plant uptake.

4. Discussion

The ammonium concentrations in the sediment estimated by the model are above the maximum concentrations of about 1 g N m^{-3} previously registered in the pore water of the Tagus intertidal sediments (Cabrita and Brotas, 2000). It should be noted that the observed value was measured for the first 5 mm of sediment and includes the ammonium consumption of benthic microalgae for primary production. No observed data were found in the literature for nutrient concentrations

in the open Tagus estuary sediments. The model results are comparable to sediment concentrations obtained for other systems (Table 4).

The values obtained for ammonium in sediments are similar to the observed range in the Tagus salt marsh sediment pore water: $1\text{--}19 \text{ g N m}^{-3}$ (Cartaxana and Catarino, 1997, 2002) and are comparable with values obtained for other salt marsh sediments (Table 4).

The model reproduces the downstream load transport and dispersion of ammonium through advection and diffusion. Thus, the ammonium concentrations in the water are reduced towards the sea, as well as in the sediments since they are in equilibrium (through molecular diffusion) with those in the water. Furthermore, since the available ammonium per unit area has been reduced downstream, there is an increase in plant ammonium uptake to satisfy the nutrient needs for growth.

The high percentage obtained for the ammonium removed by plants from the sediments is in good agreement with the observation that all nitrogen found within the depth of salt marsh roots is potentially used for plant uptake (Valiela et al., 1976; Valiela and Teal, 1979a). The different model efficiencies in ammonium uptake by C_4 and C_3 species match established patterns for C_4 photosynthesis, i.e. an enhanced photosynthetic rate and a more efficient utilization by the plant of all the resources including nitrogen (Ode et al., 1980).

In general, estuarine sediments act as a source of ammonium to the water column through diffusion along the vertical

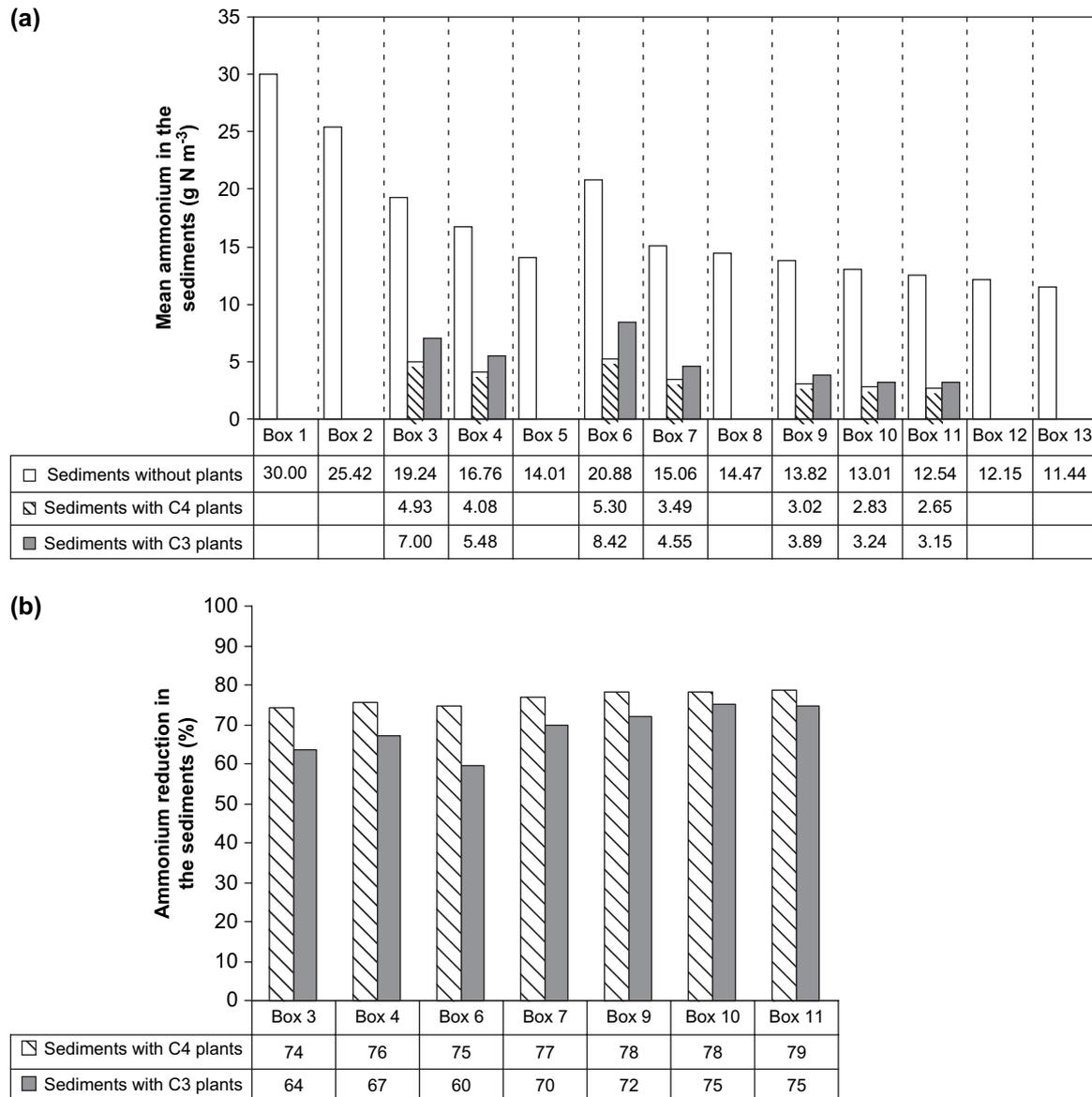


Fig. 6. (a) Mean model concentrations of ammonium in the Tagus estuarine sediments with and without salt marsh plants; and (b) percentage of the ammonium concentration reduction in the sediments due to plant uptake (for this calculation the ion concentration in the sediments without plants was considered).

concentration gradient (Rizzo, 1990). The sediments of the Tagus estuary are good examples of such systems (Cabrita and Brotas, 2000), but the model shows that salt marsh vegetation minimises the ammonium efflux to the water as stated in the literature (e.g. Flindt et al., 1999). The model results suggest that the ammonium concentrations in the water can be reduced in the entire estuary by the growth of salt marsh plants (Fig. 7).

According to Cabrita et al. (1999), the ammonium efflux from intertidal sediments in the Tagus estuary is widely variable since it is strongly dependent on the emersion period and on the tidal situation. The highest observed values were obtained in the lower intertidal area corresponding to the shorter emersion periods of the higher energy spring tides, and the lowest in the upper intertidal area in the first flood following neap tides (Table 4). Although the ammonium diffusion from the sediment is slightly higher in the upper salt marsh the difference is negligible and the estimated values

are comparable to the reported range in the Tagus estuary and other coastal systems (Table 4).

4.1. Mass balance for ammonium in sediments

A mass balance for ammonium in the upper 20 cm of the sediment was calculated for sediments with and without salt marshes (Table 5). It is important to note that this does not take into account the ammonium consumption of other “sinks” such as microphytobenthos, which plays an important role in the NH_4^+ dynamics of the first few millimetres of sediment (e.g. Cabrita and Brotas, 2000).

A simple calculation, using the gross productivity rate of the microphytobenthos (Table 6) and the C:N Redfield ratio of 45:7, gives a nitrogen uptake of 663 ton N yr^{-1} for the all estuary. This value is about three times lower than the values estimated herein for salt marsh plants, making them the major

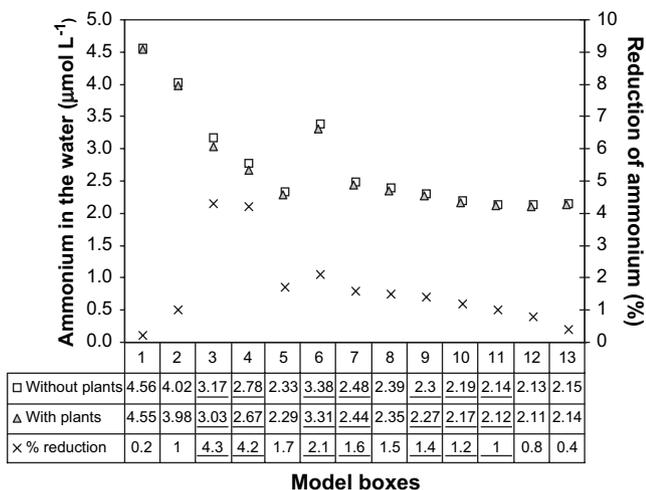


Fig. 7. Model results for the mean ammonium concentration in the water with and without plant growth simulation. Values for the boxes with salt marsh plants are underlined.

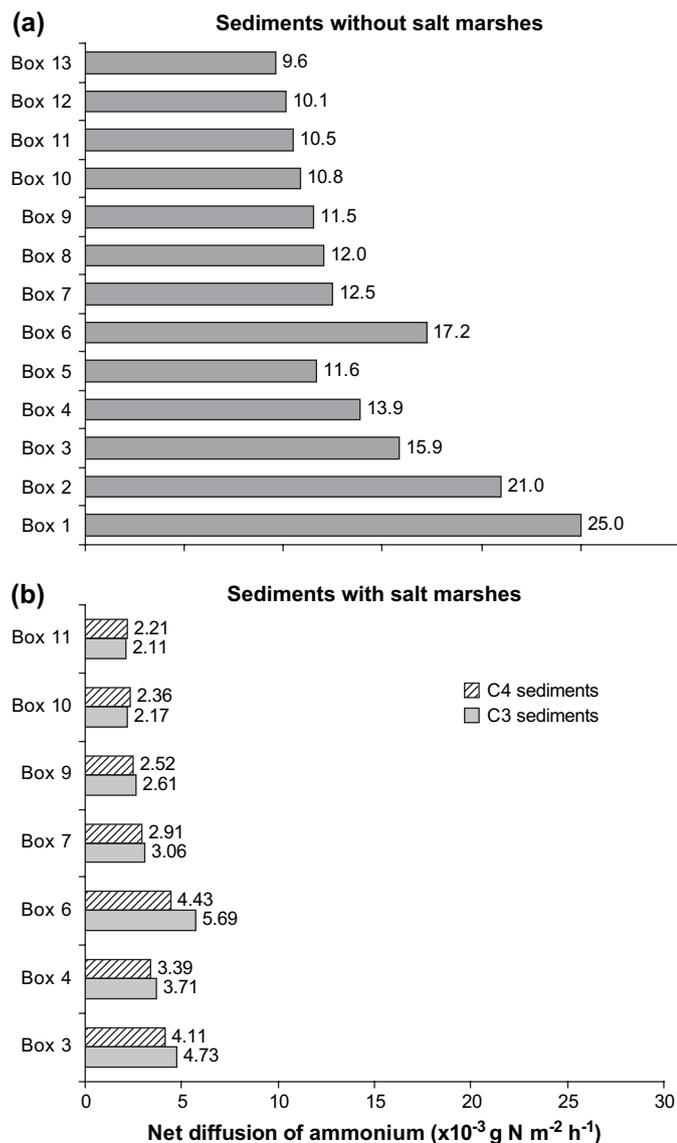


Fig. 8. Model means for the net diffusion through the sediment–water layers: (a) sediments without salt marsh plants; and (b) sediments with salt marsh plants.

Table 3

Sensitivity analysis of the annual values of plant biomass (above-ground + belowground) and ammonium concentration in the sediments to key parameters. All values are expressed as percentage deviations from the standard model

Simulated process	Variables	C ₄ total biomass		C ₃ total biomass		
		Parameter change	-10%	+10%	-10%	+10%
Nutrient uptake	Nutrient concentration of the structural parts of the cell (Q_{min})		4	-4	1	-1
	Critical nutrient concentration constant (k_c)		-3	7	-0.1	0.1
Light uptake	Half saturation constant for light (I_k)		9	-1	2	-1
Leaf mortality	Maximum leaf mortality rate (L_{max})		10	-6	8	-10
Senescence	Senescence rate (ω)		≈0	≈0	≈0	≈0
Respiration	Above and belowground respiration rates ($r_{above} + r_{below}$)		1	-0.3	≈0	≈0
	Mortality rate	Class mortality rates (μ)		44	-8	10

Variables	Ammonium in C ₄ sediments		Ammonium in sediments without plants		
	Parameter change	-10%	+10%	-10%	+10%
Diffusion coefficient of ammonium (k_{Lws})		-2	1	2	-2
Decay rate of PON to ammonium (k_{PON})		-2	2	-1	1
Ammonium sedimentation in the sediment (w_{NH_4})		3	-4	9	-8

biological sink for ammonium in the Tagus estuarine sediments. Furthermore, though salt marshes cover only 7% of the total estuarine area (as opposed to 36% colonised by benthic microalgae), the total ammonium fraction removed by salt marsh plants from the sediment should be considered as an important sink for nitrogen in the estuary. Sedimentation is the second major loss of NH_4^+ from the sediment surface layer (80% in sediments without salt marshes and 20% with salt marshes), as was also observed in other studies for nitrogen budget calculations (Valiela and Teal, 1979a). The diffusion to the water column represents only 5% of the total mineralised ammonium in the marsh. It should be emphasised that the model only takes into account the ammonium consumption by the salt marsh plants. The inclusion of the other biological and chemical sinks in the simulations is needed for the comprehensive study of the nitrogen budget in the Tagus estuarine sediments.

4.2. Carbon and nitrogen budgets in the Tagus estuary

Based on the results obtained by the salt marsh model, a comparative analysis of the role of different primary

Table 4
Observed ammonium concentrations in the sediment pore water and rates of ammonium flux at the sediment–water interface

Ammonium concentrations in the sediments pore water			
Sediment type	Site	Values (g N m ⁻³)	References
Open systems	North sea (Belgian coast)	1.4	Billen (1978)
	Conception Bay (Chile)	2.2–8.7	Farias et al. (1996)
	Satilla river estuary (US)	0.3–7.0	Jahnke et al. (2003)
Intertidal	Tagus estuary (Portugal)	0–1	Cabrita and Brotas (2000)
	Seine estuary (France)	10–35	Bally et al. (2004)
	Douro estuary (Portugal)	0.5–2.4	Magalhães et al. (2005)
	Thames estuary (UK)	0.4–1.6	Fitzsimons et al. (in press)
Salt marsh	North Carolina (US)	0.2–3.4	Mendelsohn (1979)
	Barataria bay – Louisiana (US)	4–45	Buresh et al. (1980)
	Virginia (US)	0.1–3.2	Chambers et al. (1992)
	Tagus estuary (Portugal)	1–19	Cartaxana and Catarino (1997, 2002)
Ammonium flux at the sediment–water interface			
Sediment type	Site	Values (g N m ⁻² h ⁻¹)	References
Open systems	Conception Bay (Chile)	–2.5 × 10 ⁻³ to 6.2 × 10 ⁻³	Farias et al., 1996
Intertidal	Seine estuary (France)	6.0 × 10 ⁻⁵ to 2.0 × 10 ⁻⁴	Bally et al., 2004
	Douro estuary (Portugal)	–1.4 × 10 ⁻² to 1.5 × 10 ⁻³	Magalhães et al., 2005
Salt marsh	Tagus estuary (Portugal)	Lower intertidal: 1.2 × 10 ⁻⁴ to 2.8 × 10 ⁻³	Cabrita et al. (1999)
		Upper intertidal: 4.1 × 10 ⁻⁵ to 9.3 × 10 ⁻⁵	
		Dark conditions: 7.0 × 10 ⁻⁵ to 2.0 × 10 ⁻³	
	Mira estuary (Portugal)	9.8 × 10 ⁻⁴ to 3.8 × 10 ⁻³	Cabrita and Brotas (2000)
Virginia salt marsh (US)	1.2 × 10 ⁻⁵	Lança (personal communication) Chambers et al. (1992)	

producers was performed (Table 6). Phytoplankton accounts for about 50% of the total net primary production in the estuary, while benthic primary producers (including seaweeds) are responsible for the other 50% of carbon fixation (about 25,000 ton C yr⁻¹). If net productivity per unit area is considered, C₄ plants are the most productive within the system, which together with C₃ plants account for about 25% of the total primary production within the estuary. When the gross primary production results are applied to nitrogen removal, using a Redfield C:N ratio of 45:7 in mass, the fraction of the nitrogen removed by primary production is about 80% of the total nitrogen load to the estuary. Following phytoplankton, salt marsh plants and seaweeds are the most important biological nutrient processors with similar nitrogen removal percentages. If the nitrogen load per inhabitant is considered (4.4 kg yr⁻¹; OSPAR, 2004), the total nitrogen removed from the system by salt marsh autotrophs corresponds to a loading from about 400,000 inhabitants, 20% of the population in the estuarine perimeter.

5. Conclusions

The development of the belowground growth extension to the model was essential for the simulation of plant growth and nutrient uptake. Although for some variables there is a lack of observed data, the model results were shown to be in a reasonably good agreement with the observations. Field experiments are needed for the spatial and temporal production values and for the nitrogen uptake kinetics of the main salt marsh vegetation species. Some measurements for the nutrient (ammonium) dynamics in the intertidal sediments of the Tagus were found in the literature but only a few focus on salt marsh areas. The model results show that after phytoplankton, salt marsh plants have the highest productivity in the estuary.

The integration of the salt marsh model in the ecological model as well as the additional development of the sediment nutrient object allows the analysis of the role of salt marsh plants in the ammonium dynamics of the sediment–water interface. The nitrogen uptake results for the different photosynthetic pathways classified C₄ plants as the most effective in

Table 5
Mass balance for ammonium in the sediment calculated with and without plant growth. The results correspond to the first 20 cm of sediment. The percentage of the total mineralised ammonium to each sink is in brackets

Units	Ammonium fluxes to the sediment		Sediments without plants	C ₄ sediments	C ₃ sediments
g N m ⁻² yr ⁻¹	Sources	Mineralisation in the sediment	127	120	120
	Sinks	Uptake by the salt marsh plants	0	90 (75%)	78 (65%)
		Sedimentation to the subsequent sediment layers	102 (80%)	24 (20%)	36 (30%)
		Diffusion to the water column	25 (20%)	6 (5%)	6 (5%)
Total (sources–sinks)		0	0	0	

Table 6

Values of net primary production in the Tagus estuary. Contribution to the total primary net production is in brackets

Producer types	Area ($\times 10^6$ m ²)	Net production		References
		(g C m ⁻² yr ⁻¹)	(ton C yr ⁻¹)	
C ₄ salt marsh plants	8.2	1297	10,666	This study
C ₃ salt marsh plants	12.7	150	1897	
Total salt marsh plants	20.9	150–1297	12,564 (24.9%)	Serôdio and Catarino (2000)
Microphytobenthos	115	165	3412 ^a (6.8%)	
Seaweeds	16	601–1038	8820 (17.5%)	Alvera-Azcárate et al. (2003)
Phytoplankton	320	80	25,600 (50.8%)	Ferreira (2000)
Total			50,396	

^a Net production estimated from the gross primary production value (4265 g C yr⁻¹) using a conversion coefficient of 0.8.

ammonium removal from the sediment and salt marsh vegetation as the major biological sink for ammonium in the sediments. This is observed not only through the comparison with ammonium fluxes in sediments without plants but also considering the flux to the other biological producers in the sediment (microphytobenthos).

The model suggests that the Tagus estuarine sediments act as a source of ammonium to the water column, but that its diffusion flux is minimised by the growth of salt marsh plants. Furthermore, the ammonium diffused to the water is reduced by about 15% in the Tagus salt marsh sediments.

Although the model results are in a reasonable agreement with the values observed in the field, the current model should be improved by incorporating additional biological and chemical ammonium “sinks” (e.g. microphytobenthos, nitrification and denitrification processes) to complete the nitrogen budget in the sediments and to improve the quantification of the role of salt marsh plants in the nutrient dynamics of the Tagus estuary.

C₄ salt marsh plants have the highest productivity rates among the primary producers in the estuary. Salt marsh vegetation accounts for about 25% of the total net primary production within the estuary. The model results indicate that the nitrogen removal by salt marsh autotrophs may be equivalent to the loading from about 400,000 people, which roughly represents 20% of the total population in the estuary perimeter.

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