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Allocation of nitrogen and carbon in an estuarine salt marsh in Portugal

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Abstract. Above and below-ground biomass and nitrogen and carbon composition of *Spartina maritima, Halimione portulacoides* and *Arthrocnemum perenne*, dominating species in plant communities of the lower, middle and higher salt marsh, respectively, were compared in an estuarine salt marsh in Portugal. Plant and soil nitrogen and carbon pools were estimated. For all three species root biomass was significantly higher (70 - 92 % of total biomass) than above-ground biomass. The percentage of root biomass was related to the location of the plants in the marsh: higher values were found in plants growing in the lower salt marsh where the sediment was more unstable and subject to tidal action, which stresses the role of the roots as an anchor. For all three species nitrogen concentrations were highest in leaves, reflecting the photosynthetic role of the tissue. For carbon higher concentrations were found in the stems, with the exception of *S. maritima*. In general, lower nitrogen concentrations were found in summer, which can be explained by dilution processes due to plant growth. For both nitrogen and carbon, higher concentrations were found in the soil surface layers. Higher soil nitrogen and carbon levels were associated with higher organic matter contents. Most of the nitrogen in the salt marsh occurred in the sediments (0-40 cm) and only ca. 5.7 - 13.3 % of the total was found in the plants. The greater portion (76.5 % - 86 %) of carbon was found in the sediment.

Keywords: *Arthrocnemum perenne*; *Halimione portulacoides*; Nutrient pool; Salt marsh; *Spartina maritima*; Tagus estuary.

Introduction

The Tagus estuary is one of the largest estuaries of the west coast of Europe (Fig. 1). It covers an area of ca. 32 000 ha. Its intertidal area is ca. 11 380 ha and about 1300 ha are occupied by salt marshes (Catarino et al. 1985). It receives effluents from ca. 2.5 million inhabitants living in the Lisboa area and its industries (Ca•ador et al. 1993). Reclamation of salt marsh areas together with the heavy impact of industry, urbanization and agriculture are major threats for salt marshes of the estuary.

Salt marshes occupy the transition zone between terrestrial and marine ecosystems and are characterized by a high productivity, which is considered essential in maintaining the detritus-based food chain supporting estuarine and coastal ecosystems (e.g. Odum 1961; Marinucci 1982). Coastal marshes provide habitat and nursery grounds for finfish, shellfish and waterfowl (Bellrose & Trudeau 1988; Odum et al. 1988). Wetlands, including salt marshes, have been pointed out as potential sinks for nutrients (Valiela et al. 1973; Leendertse 1995) and contaminants such as heavy metals (Banus et al. 1975; Giblin et al. 1980; Ca•ador 1994) because of their typically large plant production, high bacterial activity, anaerobic conditions and large adsorptive areas in the sediments (Valiela et al. 1976b). In view of the properties outlined above it seems imperative to invest in salt marsh conservation.

The presence and efficient cycling of nutrients is central to the development and maintenance of marshes (Langis et al. 1991). Of particular importance is nitrogen, which is considered a key nutrient in coastal ecosystems, having a critical role in determining the function and structure of salt marshes (Valiela & Teal 1979).

We initiated a study within the Tagus estuary to determine nutrient pools and fluxes on salt marsh areas dominated by different plant communities. The purpose of this work was to measure seasonal changes in biomass and nitrogen and carbon composition of *Spartina maritima, Halimione portulacoides* and *Arthrocnemum perenne*, dominating species in the lower, middle and higher salt marsh, respectively. Measurements were aimed at revealing differences between species and individual plant structures (leaves, stems and roots). Finally, the total nitrogen and carbon pools in the plant and soil compartments were estimated.

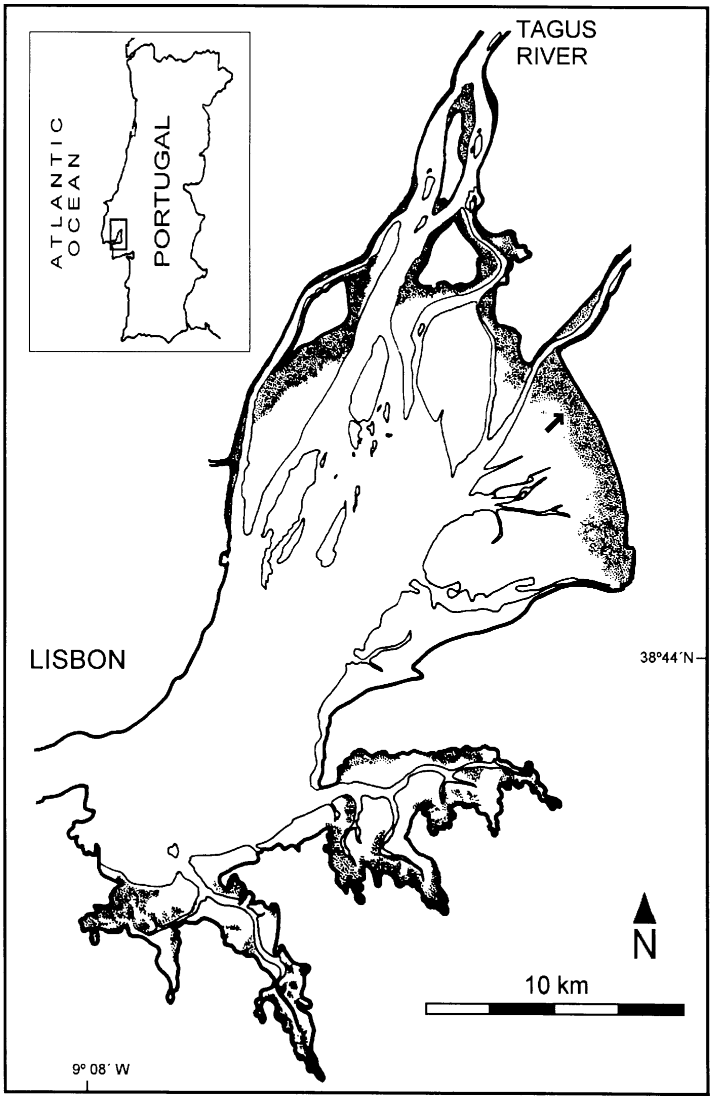

Fig. 1. Map of the Tagus estuary. Shaded areas represent salt marshes. The arrow shows the location of the studied salt marsh site. Adapted from Brotas et al. (1995).

Material and Methods

Site description

The study was conducted in the Vasa Sacos salt marsh of the Pancas area located in the eastern part of the Tagus estuary (Fig. 1). *Spartina maritima* occurs on tidal flats with daily submergence in the pioneer zone. *Halimione portulacoides* dominates the middle marsh especially along creek banks. Finally, *Arthrocnemum fruticosum* and *A. perenne* dominate the upper marsh. Plots of *Spartina maritima*, *Halimione portulacoides* and *Arthrocnemum perenne* were chosen in lower, middle and higher salt marsh, respectively.

Sample collection and chemical analysis

To quantify above-ground biomass, four quadrat samples (0.25m $\times$ 0.25m) were clipped from each plot and rinsed with water. Above-ground samples were divided into leaves (green stems in the case of *Arthrocnemum*, but referred to as ÔleavesÕ hereafter) and stems, dried (at 60 °C for 48 h), weighed and ground to a fine powder. To quantify below-ground biomass four 40-cm depth soil cores (∅ 6cm) were taken from the same plots and washed through a 0.3-mm sieve. Below-ground material retained by the mesh was, as far as possible, separated by appearance into live and dead fractions. Dead root material was usually a small fraction of the total root weight. Below-ground samples were dried (60 °C; 48 h), weighed and ground to a fine powder. Soil samples were also collected, divided into layers of 5 cm (from 0-5cm to 35-40cm), dried and, after removal of the macro-organic matter, ground to a fine powder. The samples were taken at four sampling dates spread over the year 1994. The total nitrogen and carbon concentration of each sample was determined using a CHNS/O analyser (Fisons Instruments Model EA 1108). Soil organic matter content was determined by percent weight loss after ignition (550 °C; 5 h).

Taking into account the difference in biomass and tissue element composition between species, the nitrogen and carbon pools were calculated. Soil nutrient pools were estimated to a depth of 40 cm and expressed on an area basis by determining the bulk density for each site.

Statistical analysis

The occurrence of significant differences between data was tested using two or three-way analysis of variance. Multiple comparisons among pairs of means were done using the T-method (TukeyÕs honestly significant difference method). Homogeneity of variances was tested using the BartlettÕs test. If variances were heterogeneous, data were logarithmically transformed (Sokal & Rohlf 1995).

Results

Plant biomass

For *Halimione portulacoides* and *Arthrocnemum perenne* leaf biomass increases from April onwards reaching a maximum in September and decreases from September to December (Table 1). For *Spartina maritima* the highest value is found in June decreasing afterwards and reaching a minimum in December (Table 1). Leaf biomass is lower for *S. maritima* than for *H. portulacoides* or *A. perenne* (Table 2). Stem biomass is more or less stable along the study period (data not shown). Stem biomass is higher for *H. portulacoides,* intermediate for *A. perenne* and lower for *S. maritima* (Table 2). Considering the three species, root biomass is significantly higher ($p < 0.01$) than stem or leaf biomass and ranged between 70-92% of the total biomass.

Tissue nitrogen and carbon

For the three studied species leaf total nitrogen concentrations decreases from April onwards reaching the lowest value in September and increasing in December (Table 1). Leaf total nitrogen is negatively correlated with leaf biomass (r = Ð 0.738, $p < 0.001$). Nitrogen concentration in leaves is higher in *S. maritima*, intermediate in *H. portulacoides* and lower in *A. perenne* (Table 2). Leaf carbon is much more stable during the study period than leaf nitrogen (Table 1). Leaf carbon concentrations are higher for *S. maritima*, intermediate for *H. portulacoides* and lower for *A. perenne* (Table 2). Since the variability in leaf nitrogen is much greater than that in carbon concentration, the variability in leaf C/N ratio is dominated by the variability in the nitrogen concentration of the leaves. Thus, leaf C/N ratio shows an inverse relationship to the concentrations of nitrogen: an increase in C/N ratio from April onwards, peaking in September and decreasing in December (Table 1). For stem and root nitrogen and carbon no clear seasonal pattern is apparent (data not shown). Annual means for tissue nitrogen, carbon and C/N ratio for the three species are shown on Table 2.

Considering the three species together, the nitrogen concentration is significantly higher ($p < 0.01$) in leaves,

Table 1. Leaf biomass (g/m^2), nitrogen (%), carbon (%) and C/N ratio for *Spartina maritima*, *Halimione portulacoides* and *Arthrocnemum perenne* over the year of 1994. Different letters mean significant ($p < 0.05$) differences between sampling dates.

Species	Month	Biomass (g/m^2)	Nitrogen (%)	Carbon (%)	C/N ratio
Spartina maritima	April	105.64 a	2.49 a	41.71 a	16.83 a
	June	115.08 a	2.01 b	42.19 a	21.04 ab
	September	90.56 a	1.66 b	40.21 a	24.31 b
	December	8.40 a	2.15 ab	42.81 a	19.90 ab
Halimione portulacoides	April	114.24 a	2.16 a	32.49 a	15.25 a
	June	212.52 a	1.26 b	26.82 b	21.34 b
	September	385.64 b	1.24 b	27.60 b	22.44 b
	December	138.72 a	1.87 a	35.90 a	19.25 b
Arthrocnemum perenne	April	237.28 a	1.48 a	27.61 a	18.70 ab
	June	254.76 a	1.32 ab	27.01 a	20.56 a
	September	415.72 b	1.10 b	27.29 a	25.07 c
	December	131.36 a	1.92 c	32.28 b	16.85 b

Table 2. Yearly means for biomass (g/m²), tissue nitrogen (%), carbon (%) and C/N ratio for *Spartina maritima*, *Halimione portulacoides* and *Arthrocnemum perenne*. Different letters mean significant ($p < 0.05$) differences between species.

Compartment	Species	Biomass (g/m²)	Nitrogen (%)	Carbon (%)	C/N ratio
Leaves	*Spartina maritima*	79.92 a	2.07 a	41.73 a	20.52 a
	Halimione portulacoides	212.78 b	1.63 b	30.70 b	19.57 a
	Arthrocnemum perenne	259.78 b	1.45 c	28.55 c	20.30 a
Stems	*Spartina maritima*	222.14 a	1.17 a	39.43 a	34.81 a
	Halimione portulacoides	1345.55 b	1.23 a	39.95 ab	33.01 ab
	Arthrocnemum perenne	800.04 c	1.34 b	40.93 b	30.77 b
Roots	*Spartina maritima*	3781.89 a	0.68 a	17.91 a	26.44 a
	Halimione portulacoides	7686.12 b	0.75 a	14.98 a	21.45 b
	Arthrocnemum perenne	2756.41 a	0.82 a	17.73 a	21.26 b

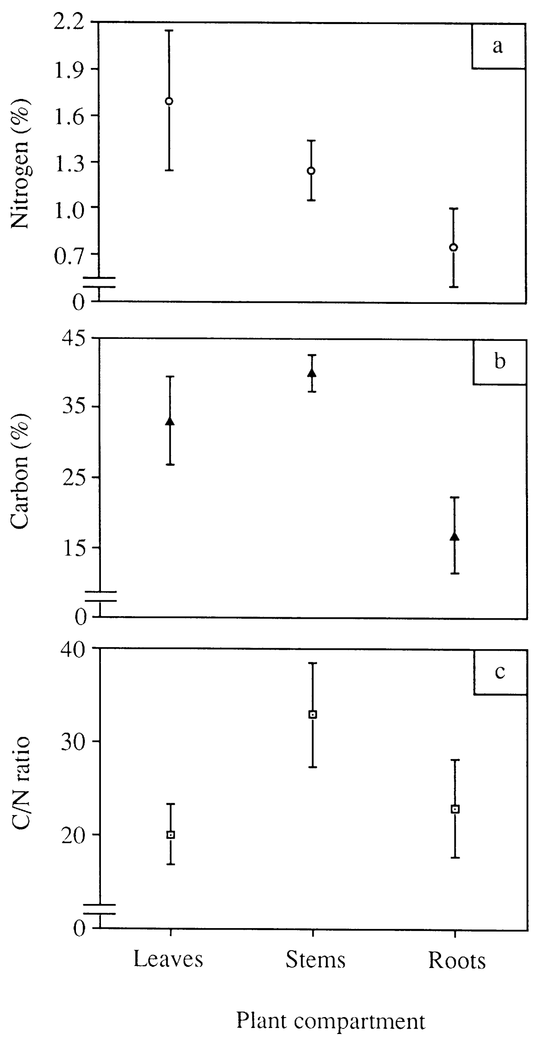

Fig. 2. Annual means (± SD) of nitrogen (a), carbon (b) and C/N ratio (c) for leaves, stems and roots (averaged from data on *Spartina maritima*, *Halimione portulacoides* and *Arthrocnemum perenne*).

intermediate in stems and lower in roots (Fig. 2a). The mean value for nitrogen concentration in *A. perenne* leaves is not significantly different as with the other two species. This may be related to the fact that in *A. perenne* no true leaves exist, but rather a photosynthetic stem. Carbon concentration is significantly higher ($p < 0.01$) in the stems, intermediate in the leaves and lower in the roots (Fig. 2b). In contrast with *H. portulacoides* and *A. perenne*, the carbon concentration in *S. maritima* stems is lower than in the leaves. C/N ratio in the different plant compartments reflects the higher concentrations of nitrogen usually found in leaves and of carbon in stems. Stems have significantly higher ($p < 0.01$) C/N ratios than leaves and roots (Fig. 2c). Leaves have significantly lower ($p < 0.01$) C/N ratios than roots in *S. maritima.*

Soil nitrogen and carbon

Soil nitrogen, carbon and organic matter content are shown in Table 3. Significantly higher nitrogen and carbon concentrations are found in the soil surface layers (Table 3). The mean values for nitrogen, carbon and organic matter content are higher in the middle marsh (0.19, 2.19 and 9.40%, respectively). Organic matter is correlated with total sediment nitrogen ($r = 0.773$; $p < 0.001$) and carbon ($r = 0.815$; $p < 0.001$).

Nitrogen and carbon pools

There are no significant differences in plant nitrogen pools during the experimental period. Although leaf biomass shows a clear seasonal pattern, the nitrogen pool did not vary significantly as there appears to be an inverse relationship between biomass and nitrogen concentration in leaves. Significantly higher ($p < 0.01$) root and stem nitrogen pools are found in the middle marsh for *H. portulacoides* as a reflection of the higher plant bio-

Table 3. Nitrogen, carbon and organic matter (%) in the different soil layers for high, middle and lower salt marsh. Different letters mean significant (p<0.05) differences between layers.

	High marsh			Middle marsh			Low marsh		
Soil layer (cm)	N	C	Org. Mat.	N	C	Org. Mat.	N	C	Org.Mat.
0-5	0.36 a	3.67 a	12.81 a	0.30 a	3.79 a	13.30 a	0.24 a	2.26 a	9.31 a
5-10	0.23 b	1.96 b	9.71 ab	0.20 b	2.40 b	9.45 bc	0.20 b	2.04 ab	8.74 a
10-15	0.18 c	1.26 c	8.25 b	0.21 b	2.67 c	10.84 ab	0.18 bc	1.90 bc	7.84 a
15-20	0.21 bd	1.32 c	8.96 b	0.19 bc	2.22 b	8.38 bc	0.16 cd	1.66 cd	7.75 a
20-25	0.12 e	1.30 c	8.20 b	0.16 cd	1.76 d	8.85 bc	0.16 cd	1.66 cd	7.39 a
25-30	0.11 e	1.18 c	8.38 b	0.15 de	1.61 de	8.46 bc	0.14 d	1.53 d	6.90 a
30-35	0.12 e	1.21 c	6.93 b	0.16 de	1.41 e	6.97 c	0.15 d	1.51 d	6.96 a
35-40	0.13 e	1.36 c	8.79 b	0.13 e	1.62 de	8.91 bc	0.15 cd	1.45 d	6.97 a

mass of this species. Significantly lower ($p < 0.01$) above-ground plant nitrogen pools are found in the low marsh dominated by *S. maritima* (Fig. 3). Annual pools for plant and soil nitrogen and carbon are shown in Table 4. The sediments in a square metre of salt marsh contain, to a depth of 40 cm, from 491 to 618 g of nitrogen. In comparison, plants account for 30.2-75.4 g N/m^2 or 5.7-13.3% of the total amount of nitrogen in the salt marsh. For carbon soil pools range from 5134 to 5721 g/m^2. Plants account for 837-1761 g C/m^2 or 14-23.5% of the total amount of carbon in the salt marsh (Table 4).

Discussion

For all three species, root biomass is significantly higher (p<0.01) than above-ground biomass and has a mean total value of 81.5%. Similar res ults to the ones reported here were obtained by Ornes & Kaplan (1989) studying *Spartina alterniflora* from a South Carolina salt marsh: 96.2 % and 83.9 % of the total biomass were roots and rhizomes of the short and tall forms, respectively. Valiela et al. (1976a) and Buresh et al. (1980) have observed that the total amount of below-ground organic matter is much higher than the aerial portion in *S. alterniflora* salt marshes. It has been suggested that this may be related to the fact that salt marsh plants colonize unstable sediments and are subject to tidal action. Thus, a developed root system can function as an anchor for the plant as well as a reservoir of energy and nutrients necessary for natural or unnatural climatic oscillation or perturbation. In agreement with this is the observation that in *S. maritima*, which colonizes the low marsh and is therefore more exposed to tidal action, the percentage root biomass (92.1 ±5.7%) is significantly higher ($p < 0.01$) than in *H. portulacoides* (82.7 ±4.7%) or *A. perenne* (69.8 ±11.8%). For *H. portulacoides*, which colonizes the middle marsh and is frequently found surrounding

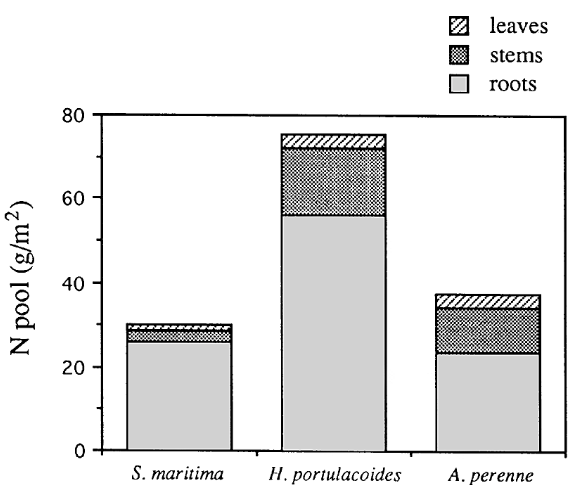

Fig. 3. Plant nitrogen pools for *Spartina maritima*, *Halimione portulacoides* and *Arthrocnemum perenne* (averaged from April, June, September, and December 1994 data).

Table 4. Annual nitrogen and carbon pools for plants and sediments of low, middle and high salt marsh. Values in g/m^2 and percentage of the total between brackets.

	Low marsh	Middle marsh	High marsh
Nitrogen			
Plants	30.2 (5.7)	75.4 (13.3)	37.8 (5.8)
Sediments	503 (94.3)	491 (86.7)	618 (94.2)
Carbon			
Plants	837 (14)	1761 (23.5)	913 (14)
Sediments	5134 (86)	5721 (76.5)	5590 (86)

the creeks, the percentage of root biomass is significantly higher ($p < 0.01$) than for *A. perenne*, which occupies the upper marsh that is infrequently flooded.

Leaf nitrogen concentrations show a clear seasonal pattern. Concentrations are higher at the beginning of the growing season and gradually decrease primarily because of a dilution of leaf nitrogen as the leaf biomass of the plant increases. This is further stressed by the negative correlation between leaf total nitrogen and leaf biomass. The fact that during summer growth plant nitrogen pools did not increase significantly, leads to the conclusion that the growth is made at the cost of plant internal nitrogen rather than by an increase of nitrogen uptake. A pattern of early accumulation may indicate that the plant stores nitrogen for later use in the growing season when nitrogen can be least available and most limiting (Hopkinson & Schubauer 1984). Bradley & Morris (1991) demonstrated that increasing salinity inhibits the uptake of new NH_4^+ in *S. alterniflora*. In summer, when salinity levels are higher because of higher temperatures, NH_4^+ uptake may be strongly restricted and growth made at the expense of internal nitrogen.

Ornes & Kaplan (1989) reported similar seasonal patterns for shoot tissue nitrogen in tall and short forms of *S. alterniflora*: lowest values during the period of July through November due to a dilution of tissue nitrogen as the aerial biomass increased during the same period. The tendency for a decrease in the percent nitrogen content of *S. alterniflora* during the active growth period has also been shown by Squiers & Good (1974) and Mendelssohn (1979). On the other hand, Morris (1982), using *S. alterniflora* cultured outdoors in continuously flowing nutrient solutions, observed a pronounced decrease to a minimum value in leaf nitrogen concentration in September in plants limited by nitrogen. Woodhouse et al. (1974), in their model predicting the yield of *S. alterniflora*, obtained a negative correlation between yield and tissue nitrogen content at the end of September. They reasoned that high concentrations of nitrogen in winter were indicative of a high growth potential while, at maturity, nitrogen concentrations were lowest in plants that had achieved the greatest growth and, hence, the greatest amount of nitrogen dilution.

The values reported here for nitrogen concentration in the leaves of *S. maritima* are higher than the ones found in the literature for *S. alterniflora* (Table 5) the dominant salt marsh species in North America. Mendelssohn (1979) reported leaf total nitrogen Ð averaged over the growing season Ð of 1.69% in tall forms of *S. alterniflora* and of 1.54% and 1.53% for medium and short forms, respectively (Table 5). Osgood & Zieman (1993) reported percent leaf nitrogen for *S. alterniflora* Ð averaged from monthly collections from May through October Ð of 1.3-1.5% (Table 5). These authors found a range of 40.7-41.8% in the carbon concentration for the leaves of *S. alterniflora* which agrees well with the annual mean value reported here for *S. maritima*. The similarity in leaf C/N ratios for the three studied species can be explained by the assumption that elements do not cycle independently in vegetation because they are involved in the basic structure and function of cells, which have similar biochemical pathways (Garten 1976). The mean value of leaf C/N ratio for the three species is 20.1. Atkinson & Smith (1983) reported a median C/N ratio of 20 analysing 92 benthic plant samples from five phyla and nine locations worldwide. According to Garten (1976), the evolution of constant ratios of elements may have been related to the maintenance of biochemical equilibria within cells that maximise protein synthesis and tissue production in natural environments.

Both leaf and stem nitrogen reported here for the three species are well above the critical concentration of 0.73 ±0.07% (below which growth would be limited)

Table 5. Reported nitrogen concentration (%) for tissues of different salt marsh plants.

Source	Species	Leaves	Shoots	Stems	Roots
This study	*Spartina maritima*	2.07		1.17	0.68
This study	*Halimione portulacoides*	1.63		1.23	0.75
This study	*Arthrocnemum perenne*	1.45		1.34	0.82
Mendelssohn (1979)	*S. alterniflora* (tall form)	1.69		-	0.87
Mendelssohn (1979)	*S. alterniflora* (medium form)	1.54		-	0.69
Mendelssohn (1979)	*S. alterniflora* (short form)	1.53		-	0.53
Hopkinson & Schubauer (1984)	*S. alterniflora*		1.05		0.44
Ornes & Kaplan (1989)	*S. alterniflora* (tall form)		1.32		0.62
Ornes & Kaplan (1989)	*S. alterniflora* (short form)		1.20		0.56
Langis et al. (1991)	*S. foliosa*		1.31		-
Osgood & Zieman (1993)	*S. alterniflora*	1.3-1.5		0.8-0.9	-

experimentally derived by Smart & Barko (1980) for *Spartina alterniflora* and *Distichlis spicata*. Stem nitrogen concentrations are also higher than the ones observed by Osgood & Zieman (1993) for *S. alterniflora* (0.8-0.9%). The annual mean values for root nitrogen in the three species (0.68-0.82%) are similar to the ones reported by Mendelssohn (1979). This author observed annual mean values of 0.87, 0.69 and 0.53% for root nitrogen in tall, medium and short forms of *S. alterniflora*, respectively (Table 5). Ornes & Kaplan (1989) reported for a 15-month period average root nitrogen concentrations of 0.62 % and 0.56% for tall and short forms of *S. alterniflora*, respectively (Table 5). Hopkinson & Schubauer (1984) found an annual mean value of 0.44% for root nitrogen in a medium-height form of *S. alterniflora* (Table 5).

The observation that higher nitrogen concentrations are found in leaves reflects the photosynthetic role of this tissue since the plants allocate more nitrogen to the leaves to support the metabolic demands of photosynthesis.

There is a decrease in nitrogen, carbon and organic matter along the soil profile. Higher soil nitrogen levels are associated with higher organic matter contents, which is not surprising since nearly all of the nitrogen found in soils is combined or closely associated with soil organic matter (Schnitzer 1991).

The average nitrogen pool of the leaf compartment is 2.74 g/m^2 which represents only 0.5% of the total nitrogen in the system. For stems the value is 9.86 g/m^2 or 1.7% of the total nitrogen. A larger portion of the nitrogen, 35.17 g/m^2 or 6% of the total, is in the below-ground plant material. The vast majority of the nitrogen in the system, 537.28 g/m^2 or 91.8% of the total, is soil nitrogen. Similar results were obtained by Buresh et al. (1980) in a Louisiana coast marsh dominated by *S. alterniflora*: they estimated the total nitrogen pool in the above-ground material at 7 g/m^2, that is, 2% of the total. The pool in the macro-organic matter of the 0-20 cm layer was 52 g N/m^2 which corresponded to 14% of the total. The soil nitrogen pool, calculated to a depth of 15 cm, was 308g/m ^{2} or 84% of the total. Langis et al. (1991) reported that the above-ground crop of nitrogen in a *S. foliosa* salt marsh was 5.93 g/m^2 in a natural and 2.11 g/m^2 in a constructed marsh, while Craft et al. (1988) observed that the relative contribution of soil macro-organic matter to the total nitrogen pool in natural and transplanted marshes along the North Carolina coast ranged between 2-22%.

In conclusion, most of the nitrogen in the salt marsh occurs in the sediments (0-40 cm) and only about 5.7-13.3% of the total is found in the plants. The greater portion (76.5-86%) of carbon is found in the sediment.

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