Available online at www.sciencedirect.com
SCIENCE DIRECT®

Acta Oecologica 24 (2003) 103–111

ACTA OECOLOGICA
INTERNATIONAL JOURNAL OF ECOLOGY

www.elsevier.com/locate/actoec

Original article

Vegetation dynamics and plant species interactions under grazed and ungrazed conditions in a western European salt marsh

Marc Tessier [a,*], Jean-Paul Vivier [b], Annie Ouin [c], Jean-Claude Gloaguen [b], Jean-Claude Lefeuvre [b]

[a] *Université Paul Sabatier Toulouse III, CESAC/CNRS (Centre d'écologie des systèmes aquatiques et continentaux), 29, rue Jeanne Marvig, 31055 Toulouse cedex 04, France*
[b] *UMR ECOBIO 6553, Université de Rennes 1, Campus de Beaulieu, 35042 Rennes cedex, France*
[c] *INP-ENSAT, Laboratoire Biodiversité dans les agro-écosystèmes, BP 107, 31326 Castanet Tolosan, France*

Received 30 August 2002; accepted 12 February 2003

Abstract

Experiments in exclosures were conducted on a salt marsh in a macrotidal system in western France. The aim of this study was threefold: (1) to compare vegetation dynamics over a period of 8 years in grazed and ungrazed conditions (2) to investigate the response of annual species to grazing duration during seedling establishment (3) to test the effect of an increase in soil nitrogen availability after cessation of grazing on interactions between *Suaeda maritima* and *Puccinellia maritima*. In grazed conditions, during all the survey, vegetation was dominated by a short *P. maritima* sward with the annual *Salicornia europaea* in the lower and middle marshes. However, after cessation of grazing in 1994, a homogeneous matrix of the forb *Halimione portulacoides*, quickly replaced *P. maritima* in the well drained lower marsh. At the middle marsh level, fine sediment and poor drainage maintained *P. maritima* while the annual *S. maritima* which tolerates taller and denser vegetation replaced *S. europaea. Elymus pungens* cover was limited till 2000 but its rising in 2001 let expect its dominance in the future. While *P. maritima* abundance remained high, spring abundance of annual species such as *S. europaea* and *S. maritima* globally decreased with sheep grazing duration on the salt marsh between February and June. Experiments with monocultures of *P. maritima* and *S. maritima* demonstrated that nitrogen was a limiting factor on the salt marsh. In a mixed community, a moderate application of nitrogen (15 g N m^{-2} $year^{-1}$ as NH_4-NO_3) promoted growth of *P. maritima* and limited the biomass of *S. maritima*, but growth of the latter was enhanced by a high application of nitrogen (30 g N m^{-2} $year^{-1}$). An increase in the abundance of annuals such as *S. maritima* on the salt marsh is discussed.

Keywords: Exclosures; Halophyte; Nitrogen addition; Plant interactions; Plant succession

1. Introduction

Salt marshes in north-western Europe are commonly grazed by sheep and cattle (Jensen, 1985; Andresen et al., 1990). Intensive grazing often results in a plant community dominated by *Puccinellia maritima* in the lower parts of the salt marsh and by *Festuca rubra* in the upper parts of the salt marsh (Ranwell, 1972; Jensen, 1985; Bakker, 1989). Grazing promotes not only perennials such as *Puccinellia maritima*, but also annuals such as *Salicornia europaea*, although trampling by livestock has been observed to damage *Salicornia europaea* seedlings (Jensen, 1985; Kiehl et al., 1996). Cessation of grazing modifies both the disturbance regime and interactions between plant species. Grazing experiments designed to study both long-term (Jensen, 1985; Andresen et al., 1990; Van Wijnen et al., 1997) and short-term (Kiehl et al., 1996) shifts in plant species assemblages on the Wadden Sea salt marshes have demonstrated that cessation of grazing at low stocking-rates results in a progressive replacement of *Puccinellia maritima* and *F. rubra* dominated communities by monospecific stands of *Halimione portulacoides* in the lower marsh and *Elymus pungens* (=*Elymus athericus*) in the upper marsh (Jensen, 1985; Andresen et al., 1990; Van Wijnen et al., 1997). Experimental studies of this kind are

* Corresponding author.
E-mail address: marc.tessier@ecolog.cnrs.fr (M. Tessier).

DOI: 10.1016/S1146-609X(03)00049-3

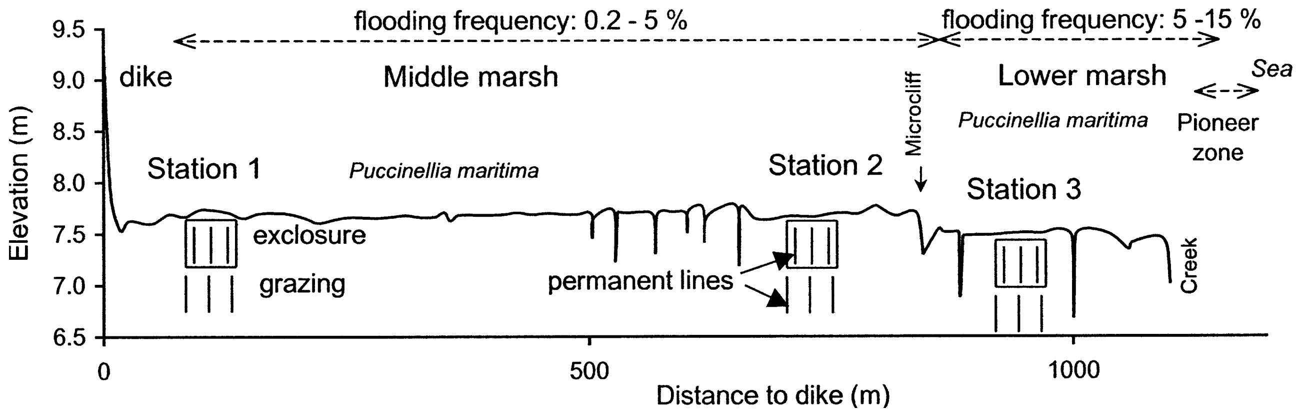

Fig. 1. Diagram of the three exclosures (Stations 1 to 3) along the transect (from Bonis et al., 2000; Lefeuvre et al., 2000). Flooding frequency is the number of days of flooding per year.

necessary to allow prediction on vegetation dynamics at a large scale (e.g. in abandoned salt marshes) and as such to propose appropriate management strategies (Bakker, 1989; Kiehl et al., 1996) in similar tidal systems of north-western Europe.

Cessation of grazing means a direct change to the disturbance regimes in salt marshes leading subsequently to changes in vegetation composition and nutrient availability which, in turn, could modify species interactions. In fact, the growth of salt marsh plants is often limited by a lack of nutrients and particularly of nitrogen (Jefferies, 1977; Jefferies and Perkins, 1977; Kiehl et al., 1997; Van Wijnen and Bakker, 1999; Van Wijnen and Bakker, 2000) as has been observed in the annuals *Suaeda maritima* and *Salicornia europaea* growing in British salt marshes (Pigott, 1969; Stewart et al., 1972). In Mont-Saint-Michel Bay, France, cessation of sheep grazing has been related to an increase in N-mineralization (Vivier, 1997). Raising of N-mineralization increases the availability of nitrogen typically leading to greater N-uptake by plants (Kaye and Hart, 1997), thus potentially altering the dominance of species present. This has been observed along the Wadden Sea coast, where Kiehl et al. (1997) recorded the replacement of *Puccinellia maritima* by *Suaeda maritima* following the addition of high doses of nitrogen (25 g m^{-2} $year^{-1}$).

The present study was conducted in a western European macrotidal system. It focused on annual species which respond quickly to disturbance (Tessier et al., 2002) and which are abundant both in grazed conditions and in the first years following cessation of grazing (Kiehl et al., 1996). This study investigated (1) the vegetation dynamics over 8 years of grazed and ungrazed salt marshes in a macrotidal system (2) the effect of heavy grazing on the demography of annual species (3) the effects of change in nitrogen availability on the interaction between the perennial *Puccinellia maritima* and the annual *Suaeda maritima*.

2. Materials and methods

2.1. Study area

The study was carried out in the salt marshes of Mont-Saint-Michel Bay, in western France, between Normandy and Brittany (48°40'N, 1°35'W). In this area, the tidal range is the highest in Europe with an average of 10–11 m and a maximum of 16 m during storm events. These salt marshes were traditionally grazed by sheep leading to an impoverished community dominated by the perennial *Puccinellia maritima* in association with the annual *Salicornia europaea* (Guillon, 1984; Bouchard et al., 1995). Large areas of salt marshes have now been abandoned and have "natural" communities dominated by the perennials *E. pungens* and *H. portulacoides* (Bouchard et al., 1995; Tessier et al., 2000; nomenclature of plant species follows Tutin et al., 1964–1980). These ungrazed salt marshes are currently increasing in surface area.

The study site was located in a heavily grazed area dominated by *Puccinellia maritima*. The stocking rate was around 4.5 sheep ha^{-1} in 1980 (Guillon, 1980) but is now 7 sheep ha^{-1} due to an increase in flock size with a peak of 10 sheep ha^{-1} during the summer months following the birthing (Vivier, 1997).

The entire area is drained by a network of tidal creeks. The soil is composed of a mixture of clay and fine marine sand.

2.2. Long-term recording of vegetation

In January 1994, three stations were established along a transect running from the seawall to the intertidal flats (Stations 1, 2 and 3; Fig. 1). Elevations of the three stations above the mean sea level were 7.69 m for Station 1, between 6.71 and 6.92 m for Station 2, 6.61 m for Station 3. Stations 1 and 2 were considered to be situated in the middle marsh. Station 1 had a poorer drainage system than Station 2 and was flooded more frequently (around 5% and 0.2% of the year, respectively). Station 3 was in the lower marsh where the soil

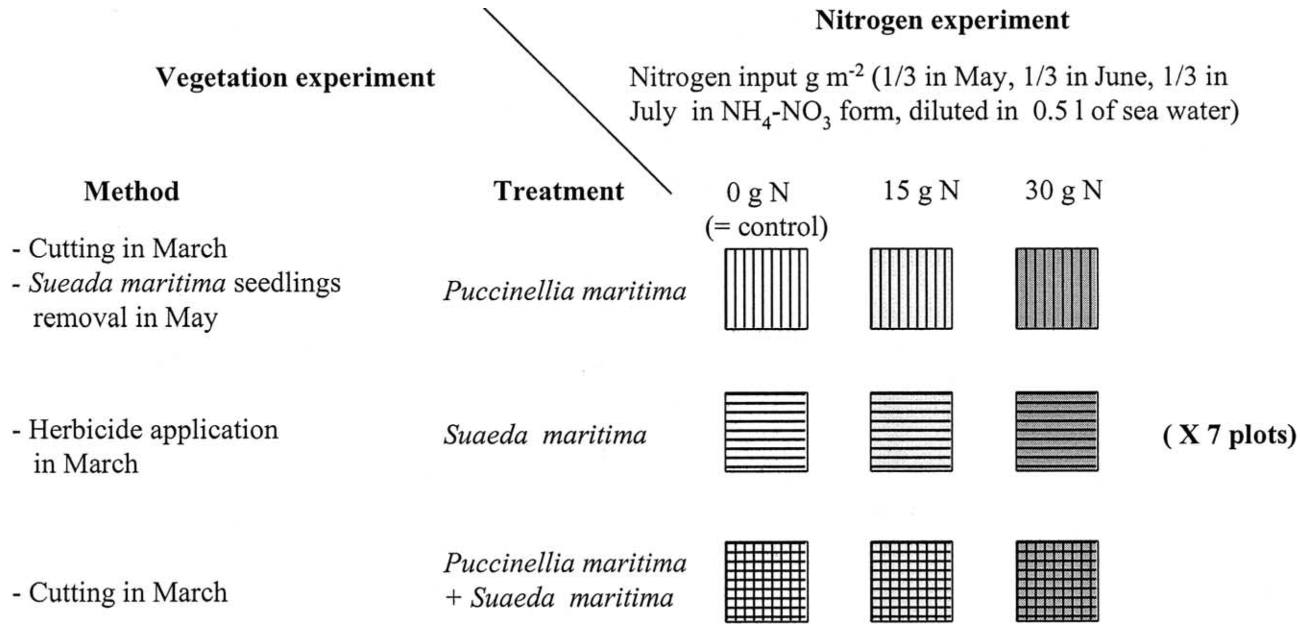

Fig. 2. Summary of the nitrogen application experiment on monocultures of *Puccinellia maritima*, *Suaeda maritima* and on mixed treatment of both species.

was more sandy than in the other two sites. The median grain size of sediments at Stations 1, 2 and 3 were 13.8, 17.5 and 23.4 µm, respectively, while the sedimentation rates between 1 October 1998 and 4 April 2000 (18 months) were 21.16, 10.26 and –1.57 mm, respectively (Bonis et al., 2000).

At each station, one 15 × 15 m exclosure was established. The fence allowed small herbivores (rabbits, hare) and geese to enter the exclosure although these animals were very rare in the study area. Plant cover was recorded annually from 1994 to 2001 using the point contact method (adapted from Gounot, 1969) along three 10 m permanent lines which were set up 4 m apart from one another, in grazed conditions (outside exclosure) and in ungrazed conditions (inside exclosure). Species contacts (presence or absence) were recorded every 10 cm along each of the permanent lines (=100 points per line, =300 points per treatment) in September when all species were fully developed. The percentage coverage of each species encountered was calculated as follows: positive contacts for a species/300. Species with less than 5% coverage throughout the experiment are not included in the figures.

2.3. Impact of grazing duration on plant dynamics

In Station 2, on the 15th of each month from February to June 1994, the exclosure fence was moved back by 4 m into the grazed area. Each date of fence shifting, corresponded to a subplot. Hence, we obtained 5 subplots corresponding to 1, 2, 3, 4, 5 months of grazing duration during seedling establishment. This experiment was not conducted in Stations 1 and 3 because of the presence of tracks, creeks and/or hunter hide-outs prevented the extension of exclosures. For the same reason, no replicate was conducted in Station 2. Consequently, the lack of replication did not allow statistical analysis and thus limited the significance of the results. Contact readings were made in January (prior to seedling emergence) and in July 1994 (following seedling emergence) for each subplot, using the point contact method, (three transects of 10 m which were 1 m apart) for each species.

2.4. Nitrogen fertilisation experiment

Experimental nitrogen fertilisation was conducted at Station 1 in 1998 (Fig. 2). This station was chosen because no tide covered the exclosure between the first application of nitrogen in May and plant harvesting in September. Nitrogen application (0, 15, 30 g m^{-2} $year^{-1}$) and vegetation state (a mixture vs. a monoculture) were applied factorially in seven replicated blocks containing nine quadrats (Fig. 2). Treatments were assigned to block according to a randomised block design.

Large monospecific stands of *Puccinellia maritima* were present in the 15 × 15 m exclosures in February 1998. Seven blocks (5 × 2 m) of nine quadrats (40 × 40 cm) were established randomly on the *Puccinellia maritima* matrix. Quadrats were 40 cm apart and located at least 50 cm away from the permanent line to avoid interference. In order to enhance the emergence of *Suaeda maritima* seedlings, during the month of March, in each block, *Puccinellia maritima* was cut in six of the nine quadrats to obtain a homogenous sward with a height of about 4 cm. In three of the quadrats with cut *Puccinellia maritima*, young plants of *Suaeda maritima* were manually removed following germination in May. We obtained three quadrats with a monoculture of *Puccinellia maritima* and three quadrats with a mixture of the two species. A non-remnant herbicide (glyphosate) was applied in March to the three remaining quadrats. The vegetation was killed but germination occurred soon after and in May, we obtained three quadrats with a high density monoculture of *Suaeda maritima*.

In May, three groups of three quadrats corresponding to the three treatments (*Suaeda maritima* monoculture, *Puccinellia maritima* monoculture and both species mixed) were selected randomly for nitrogen addition. A nitrogen solution (NH_4-NO_3) was applied in two groups of quadrats which received 15 and 30 g m^{-2} $year^{-1}$, respectively. Half a litre of nitrogen solution mixed with sea water was applied three times to each quadrat in May, June and July (Fig. 2). The quadrats of the third group were the controls and received half a litre of sea water.

In order to avoid edge effects, the above-ground biomass was cut in September in 25 × 25 cm sub-quadrats placed in the middle of the 40 × 40 cm quadrats. Each species was weighed separately in the mixed culture. Plant material was dried at 68 °C for 72 h and weighed.

Since the data were normally distributed, the effects of vegetation state and nitrogen addition on biomass yield were analysed for each of the species by application of the means of Generalized Linear Model (GLM), incorporating block effects. When a factor was significant, means were tested for significant differences using the LSD test for each modality of the other factor. However, when significant interaction effects were found, the LSD test was applied only to the interactions.

3. Results

3.1. Vegetation dynamics under grazed and ungrazed conditions

Under grazing pressure, vegetation was dominated by *Puccinellia maritima* at all stations (Fig. 3). *Salicornia europaea* cover increased greatly from 1994 to 1996 but showed a decrease after 1997 except at Station 3. *Suaeda maritima* was absent in 1994 in the grazed area but appeared at Station 3 in 1995, at Station 2 in 1996 and at Station 1 in 1997. At the three stations where the vegetation was dominated initially by *Puccinellia maritima* in 1994, it subsequently became a mixed community with *Spergularia* spp., and the annuals *Salicornia europaea* and *Suaeda maritima* appearing.

After cessation of grazing in January 1994, *Salicornia europaea* showed increase in cover compared with grazed areas at Stations 1 and 2 (Fig. 3). *Salicornia europaea* disappeared in 1995 and 1996, while *Suaeda maritima* replaced it after 1 year at Stations 1 and 3 and after 2 years at Station 2. *Suaeda maritima* decreased and disappeared at Stations 1 and 3 in 1999 and in 1998, respectively, but not completely at Station 2. In 2000 and 2001, annuals were scarce.

Perennial species such as *Triglochin maritima* and *Aster tripolium* tended to increase slightly just after cessation of grazing. *Puccinellia maritima* cover declined meanwhile with an increase in *H. portulacoides* cover first at Station 3, then at Station 2 and subsequently at Station 1 (Fig. 3). In Station 3, the original vegetation was completely replaced by a monospecific stand of *H. portulacoides* in 1999. At Stations 2 and 1, *E. pungens* and *F. rubra* were recorded from 1998 and 1999, respectively, and their cover increased up to 2001.

3.2. Impact of grazing duration on plant dynamics

At Station 2, the percentage coverage in July of *Salicornia europaea* and *Suaeda maritima* decreased when exclosure establishment was postponed from February to May (Fig. 4). However, only one month of exclosure (June exclosure) lead to a higher *Salicornia europaea* cover than 2 months (May exclosure). After 5 months of exclosure, the cover of *Puccinellia maritima* was at its lowest with 90% cover, while *Salicornia europaea* cover reached its maximum (53%). *Spergularia* spp. seemed to reach its highest cover after 4 months of exclosure.

3.3. Nitrogen fertilisation experiment

The effect of nitrogen addition was significant for both *Puccinellia maritima* and *Suaeda maritima* (Table 1). However, vegetation state (monoculture vs. mixture) and the interactions between nitrogen addition and vegetation state were only significant for *Suaeda maritima*.

In monoculture and mixed stand conditions, the mean dry weight of *Puccinellia maritima* increased significantly ($P < 0.05$) between controls and quadrats with a 15 g m^{-2} input of nitrogen (Table 2). In monoculture, mean dry weight did not increase further when 30 g m^{-2} additions of nitrogen were applied. Whereas, in mixed stand conditions biomass decreased such that the mean dry weight was not significantly different than that of the control.

Taking into account the interaction between N addition and vegetation state, mean dry weight of *Suaeda maritima* differed significantly in all cases except in the mixed stand between quadrats with 0 and 15 g m^{-2} of nitrogen added and in monoculture between quadrats with 15 and 30 g m^{-2} (Table 2).

4. Discussion

4.1. Effects of grazing and trampling on plant demography

At all stations, under grazed conditions, the vegetation was dominated by a sward of *Puccinellia maritima* with the annual species *Suaeda maritima* and *Salicornia europaea*. These three species, generally also occurring in the ungrazed lower marsh, may have benefited from an increase in salinity and bare areas caused by grazing as demonstrated by Bakker (1985). Perennial species such as *Spergularia spp.* in the middle marsh (Stations 1 and 2) and *T. maritima* forming small patches in the upper part of the salt marsh (Station 1) were only moderately promoted by grazing. On the other hand, they may have suffered from grazing e.g. *H. portulacoides* which was scarce in the lower marsh (Station 3). The absence of upper marsh species and the vegetation pattern

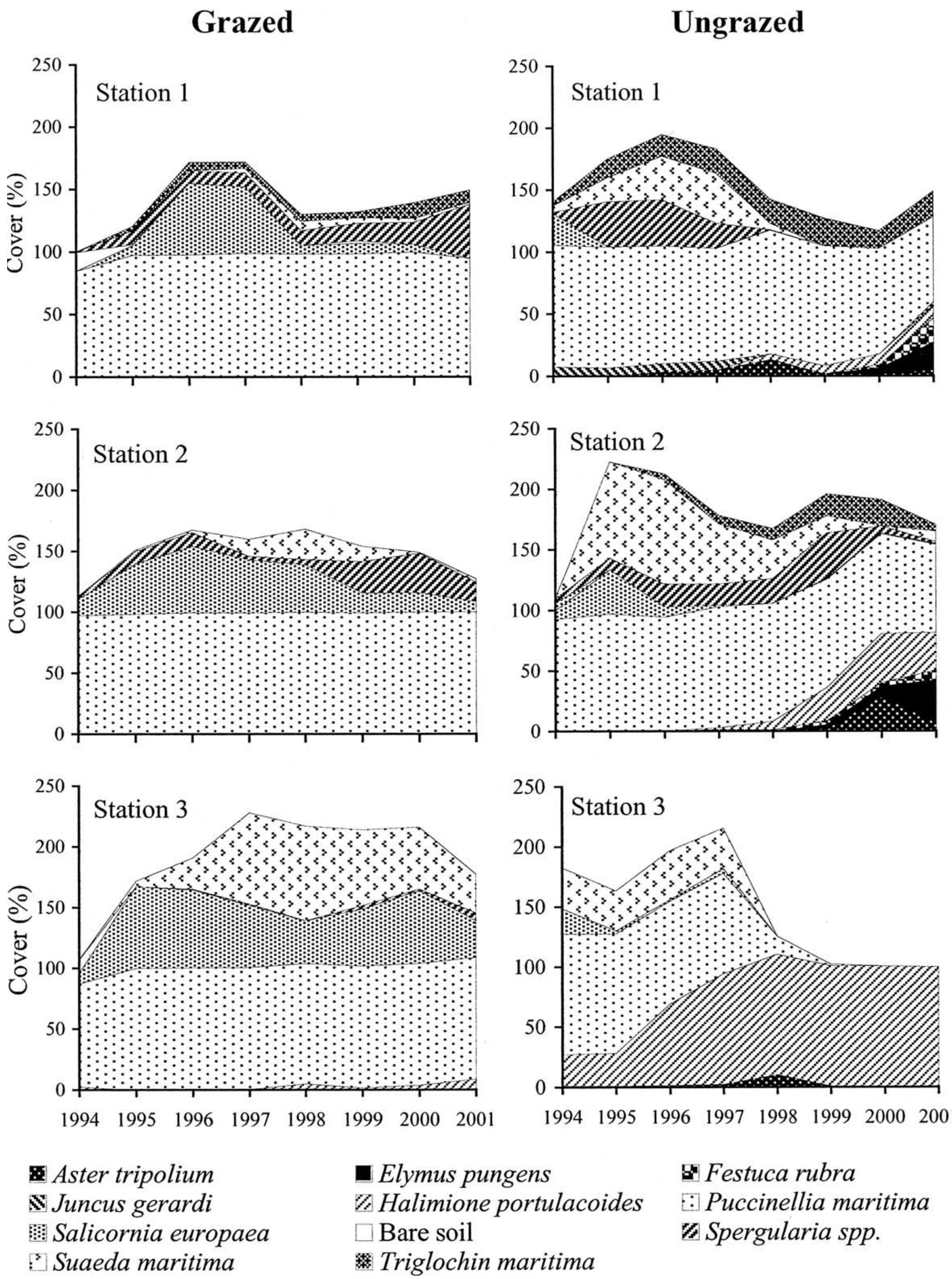

Fig. 3. Changes in plant composition between 1994 and 2001 in grazed conditions (left) and ungrazed conditions (right) in Stations 1, 2 and 3 using the point contact method.

was similar to other western European salt marshes with heavy sheep grazing (Ranwell, 1972; Jensen, 1985; Bakker, 1989; Adam, 1990; Kiehl et al., 1996).

Grazing promoted largely *Salicornia europaea* which was the dominant annual to emerge from the perennial matrix. It created open space suitable for *Salicornia europaea* seedlings but it also damaged plants as a result of trampling (Jensen, 1985; Kiehl et al., 1996). Our results showed that spring abundance of *Salicornia europaea* depends on sheep grazing duration (=trampling duration) on the salt marsh between February and June. Trampling led to the lowest *Salicornia europaea* cover in July after exclosure establish-

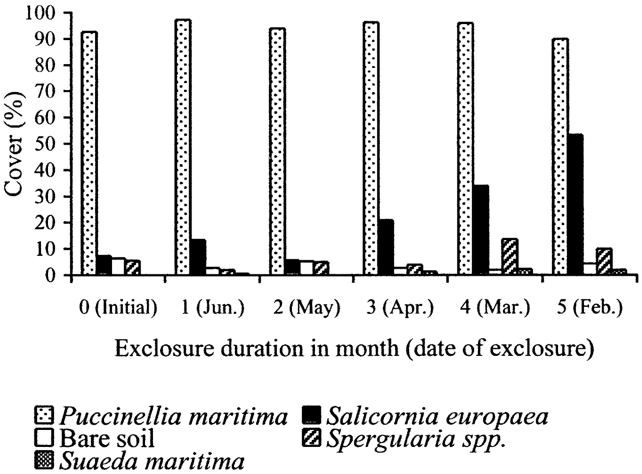

Fig. 4. Effect of grazing duration on species cover in July. On the x coordinate, "initial" corresponds to the initial state of vegetation in January while the month is the date of exclosure (from February to June 1994).

ment in May (5.7% cover value) in spite of a high potential (53.3% cover after exclosure erected in February). In fact, many young and fragile seedlings progressively germinated until May and were damaged by sheep trampling. The quantitative impact of trampling on *Salicornia europaea* seedlings should be measured in other salt marshes so much more that our experiments lack of replications.

Paradoxically, it seemed that late grazing enhanced the survival of *Salicornia europaea*, which was more abundant in July after 1 month of exclosure establishment (June establishment) than after 2 months (May establishment). Grazing appeared to be beneficial for the establishment of plant species by reducing the height of canopy in spring and thus, seedling mortality (Bakker and De Vries, 1992). Moreover, their fragility decreased while their size increased. Finally, the cover of *Salicornia europaea* in September 1994 (Fig. 3) was higher after cessation of grazing at Stations 1 and 3 than in grazed conditions, but not at Station 2. There is some evidence to suggest that competition interactions with the perennials was stronger at Station 2 and had limited *Salicornia europaea*'s emergence.

Trampling had a great impact on demography of seedlings of *Salicornia europaea* but it had no effect on its final cover.

4.2. Vegetation dynamics after cessation of sheep grazing

The vegetation dynamics just after cessation of sheep grazing is conducted by seedling recruitment from seed bank (and from seeds input by flooding) and clonal expansion of perennials.

In salt marshes seedling recruitment depends greatly on salinity and perturbations due to flooding (Ungar, 1998). Studies completed in Mont-Saint-Michel Bay have demonstrated that *Suaeda maritima* tolerates saline conditions and most of the seeds in the seed bank will germinated in the spring (Tessier et al., 2000). Moreover, the transient seed bank of *Suaeda maritima* can be supplied by a high seed production and a large input from flooding (Tessier et al., 2002). This explains the high abundance of *Suaeda maritima* particularly at the lower marsh (Station 3) in spite of high salinity caused by frequent flooding. Additionally to these constraints, some studies have shown that animal grazing leads to a differential decline in the species seed banks. Foraging by Lesser Snow Geese leads to a reduction in vegetation cover and thus, to a decline in the relative abundance of seeds of species characteristic of ungrazed vegetation (Chang et al., 2001). In a heavily grazed salt marsh in South Wales dominated by *Puccinellia maritima* the two species *Salicornia europaea* and *Suaeda maritima* composed 100% of the seed bank while in ungrazed or lightly grazed marshes seeds of other species (*Spergularia marina*, *T. maritima* and *Juncus gerardi*) were numerous (Ungar and Woodel, 1996). In our study area where heavy grazing occurred, the seedling recruitment of *Spergularia spp.*, *Salicornia europaea* and *Suaeda maritima* was efficient while the impoverishment of the seed bank of other species could explain their low abundance after grazing cessation. Indeed, species such as *J. gerardi* and *T. maritima* even if they could have a persistent seed bank in ungrazed conditions (Hutchings and Russell, 1989), were probably absent from the seed bank in our study and seemed to develop in the first year after exclosure only by clonal expansion in the middle marsh.

Table 1
Effect of Nitrogen (N) and vegetation state (monoculture, mixture) on dry aboveground biomass of *Suaeda maritima* and *Puccinellia maritima: F*-values of a two way ANOVA with block factor

	d.f.	*Suaeda maritima*	*Puccinellia maritima*
N	2	17.87* * *	18.85* * *
Vegetation state	1	217.00* * *	0.97
N × vegetation state	2	5.64* *	2.087
Block	6	0.28	0.92

* * $P < 0.01$,
* * * $P < 0.001$.

Table 2
Dry aboveground biomass (g m^{-2}) of *Suaeda maritima* and *Puccinellia maritima* in monoculture and mixed communities. Since significant interactions was found for *Suaeda maritima* between Nitrogen addition and Vegetation state, equal letters (from a to c) indicate that differences between *Suaeda maritima* biomass are not significant (LSD test, $P > 0.05$). Equals letters x and y for monoculture and α to β for mixture (no interactions between Nitrogen addition and Vegetation state) indicate that differences between *Suaeda maritima* biomass are not significant difference between means after Nitrogen addition in monoculture and in mixed communities for *Puccinellia maritima* (LSD test, $P < 0.05$)

Nitrogen addition (g m^{-2})	*Suaeda maritima* biomass		*Puccinellia maritima* biomass	
	Monoculture	Mixture	Monoculture	Mixture
0	1072 ± 101 a	128 ± 46 c	657 ± 46 x	647 ± 68 a
15	1787 ± 108 b	99 ± 48 c	1149 ± 88 y	1219 ± 107 b
30	2002 ± 149 b	552 ± 174 d	1102 ± 115 y	832 ± 115 a

Other species, scarce and absent from the site such as *F. rubra* and *E. pungens*, respectively, and with probably any persistent seed bank could have established by seeds, coming from adjacent areas, after few years.

In the upper part of the marsh (Station 1) *Puccinellia maritima* remained dominant throughout the experimental period and was not replaced by upper marsh species even following the cessation of sheep grazing. In salt marshes where grazing has been abandoned, *Puccinellia maritima* is generally associated with waterlogged and poorly aerated soil (Gray and Scott, 1977), caused by a fine sediment texture (Bonis et al., 2000). Those conditions occurred in Station 1 due to the light topographic level increase between the sea-wall and the middle marsh and then its decrease towards the sea (Fig. 1). This "inverse slope", resulting from the embankment construction limits drainage of the upper marsh. Handa et al. (2002) showed that clonal species propagation in the context of natural re-vegetation on coastal marsh occur only where edaphic conditions are suitable. These edaphic conditions occurring at Station 1 (fine sediment and poor drainage) seemed to be unsuitable for the establishment of *H. portulacoides*. At Station 3, after cessation of grazing, *Puccinellia maritima* was quickly replaced by a monospecific stand of *H. portulacoides* near the intertidal flats although this species usually occurs in ungrazed upper parts of salt marshes (Jensen, 1985; Van Wijnen et al., 1997; Tessier et al., 2000). The proximity of creeks and the sandy texture of soil provided a good drainage favourable to this species (Beeftink et al., 1978). Moreover, in grazed and ungrazed plots of the lower marsh station, small individuals of *H. portulacoides* were numerous in 1994. In the former, they were kept at low coverage by grazing, however, in the latter, cessation of sheep grazing lead to a high abundance. At Station 2, edaphic conditions were intermediate and the expansion of *H. portulacoides* seemed limited but less than at Station 1.

At Stations 1 and 2, *E. pungens* and *F. rubra* presented few small patches in 2000 which spread substantially in 2001. They may replace *Puccinellia maritima* in the future as suggested by Olff et al. (1997) who showed that *Puccinellia maritima* and *Plantago maritima* were gradually replaced during succession by *E. pungens* especially in the mid and upper salt marsh. However, the spread of *E. pungens* and *F. rubra* may be limited at Station 2 by *H. portulacoides* which is well adapted to competition (Dormann et al., 2000) and by the poor drainage occurring at Station 1. The vegetation monitoring in exclosures in the future will give more information.

The pattern of change was consistent with that observed in the North Sea where a microtidal regime occurs (Jensen, 1985; Kiehl et al., 1996). The macrotidal regime which occurred in the Mont-Saint-Michel Bay did not seem to influence succession of perennial species after cessation of grazing.

After cessation of grazing, *Salicornia europaea* was rapidly eliminated as a result of the reduction of bare soil (Bakker and De Vries, 1992); this species was quickly replaced by *Suaeda maritima* which tolerates taller and denser vegetation than *Salicornia europaea*. These annual species remained abundant between 1995 and 1997 but decreased after 1997. Annual species showed both in grazed and ungrazed conditions great fluctuations in their abundance during the experiment. Grazing intensity and increase in the nitrogen availability were expected to explain these fluctuations.

4.3. Effect of nitrogen application

While *Puccinellia maritima* did not respond significantly to the interaction between vegetation state and N addition, *Suaeda maritima* biomass showed significant differences when interactions between the two factors were tested. The reproductive strategies of both plants (the former is perennial, the latter is annual) might explain their contrasting behaviour. Additional studies are needed to elucidate the mechanisms underpinning both responses.

In monoculture, the biomass of *Suaeda maritima* and *Puccinellia maritima* increased greatly after nitrogen application, even with a moderate input of nitrogen (15 g m^{-2}). As has been observed in other salt marshes, nitrogen appears to limit plant production (Valiela and Teal, 1974; Jefferies, 1977; Jefferies and Perkins, 1977; Leendertse, 1995; Kiehl et al., 1997).

In the mixed community, at the highest nitrogen input (30 g m^{-2}) *Puccinellia maritima* biomass increased only slightly while *Suaeda maritima* growth was strongly promoted. Kiehl et al. (1997) noted a decrease in *Puccinellia maritima* biomass after high nitrogen application (25 g m^{-2}), that was caused by competition for light with *Suaeda maritima*, which overshadows *Puccinellia maritima*. Scholten et al. (1987) noted that *Puccinellia maritima* was the dominant species where there was a low nitrogen input. In our experiment, with a moderate input (15 g N m^{-2} $year^{-1}$) the biomass of *Suaeda maritima* was much lower than in monoculture conditions. A moderate nitrogen application promoted *Puccinellia maritima* growth which efficiently limited the growth of *Suaeda maritima*.

N-mineralization was higher in ungrazed than in grazed salt marshes. This has been attributed by Van Wijnen et al. (1999) to herbivores (geese, hare and rabbits), that by preventing litter accumulation, reduce mineralization rates. The mineralization potential in the middle marsh of the Mont-Saint-Michel Bay was estimated to be 7 g N m^{-2} $year^{-1}$ in grazed conditions and 16.1 g N m^{-2} $year^{-1}$ in ungrazed conditions (Vivier, 1997). This increase in N-mineralization does not seem to be sufficient to explain the dramatic increase in *Suaeda maritima* cover measured in ungrazed conditions. Indeed, there is a very big difference between the increase in N-mineralization in the field (9.1 g N m^{-2} $year^{-1}$) and the level of N addition needed to promote *Suaeda maritima* (25–30 g m^{-2}) in experiments. Moreover, while *Suaeda maritima* abundance increased in ungrazed conditions, *Salicornia europaea* cover in the sheep-grazed conditions also increased. Thus, we may assume that others factors promoted annual species. This period (approximately 1995–1998) favourable for annual species was marked by a succession of events which occurred in the Mont-Saint-Michel Bay: (1) early 1995 was characterised by a series of storm events. In a macrotidal regime, the effect of waves on sediment and vegetation removal is amplified during a storm. Thus, the succession of storms in 1995 removed sediment from the intertidal flats (Radureau, unpublished data) and created patches in the exclosure where *Suaeda maritima* occurred as a monoculture. (2) After this stormy period, the sedimentation rate on the salt marsh was higher between 1996 and 1998 at Stations 1 and 2 than in 1999–2000 period (Jigorel, unpublished data). It resulted in a higher mineral nitrogen input into the salt marsh (Van Wijnen and Bakker, 1997). Moreover, sheep faeces and organic matter deposits were observed in the exclosures where the tall vegetation retained them. This input of organic nitrogen could also explain the high abundance of *Suaeda maritima*.

5. Conclusion

Grazing caused significant disturbance on the salt marsh which greatly influenced the demography of *Salicornia europaea* seedlings and resulted in the dominance of the perennial *Puccinellia maritima* from the seawall to the lower marsh. After cessation of grazing, competitive interactions led to rapid or progressive changes in plant composition in the lower and middle marsh, respectively. *Puccinellia maritima* cover remained high during the exclosure experiment in the middle marsh. Changes in nutrient availability and some disturbances interfered with these dynamics and seemed to promote annual species such as *Suaeda maritima*. Nitrogen accumulation resulting of litter accumulation (Van Wijnen et al., 1999), led to the replacement of *Puccinellia maritima* by *E. pungens*. An increase of this species may be expected in the future except in some depressions created by the “inverse slope”. The colonisation of *E. pungens* could be enhanced by exogenous nitrogen inputs from atmospheric deposition (Bakker and Berendse, 1999).

Acknowledgements

We thank Dr. N. Barsoum, Dr. V. Bouchard, Dr. E. Feunteun and Dr. Y. Frenot for comments on an earlier version of this manuscript. We are grateful to two anonymous reviewers who gave valuable comments on earlier versions of the manuscript. This study was funded by the ELOISE RTD European programme, no. 316991 MVB 341.

References

Adam, P., 1990. Saltmarsh Ecology. Cambridge University Press, Cambridge.

Andresen, H., Bakker, J.P., Brongers, M., Heydemann, B., Irmler, U., 1990. Long-term changes of salt-marsh communities by cattle grazing. Vegetatio 89, 137–148.

Bakker, J.P., 1985. The impact of grazing on plant communities, plant populations and soil conditions on salt-marshes. Vegetatio 62, 391–398.

Bakker, J.P., 1989. Nature management by grazing and cutting. Kluwer Academic Publishers, Dodrecht.

Bakker, J.P., Berendse, F., 1999. Constraints in the restoration of ecological diversity in grassland and heathland communities. Trends Ecol. Evol. 14, 63–68.

Bakker, J.P., De Vries, Y., 1992. Germination and early establishment of lower salt-marsh species in grazed and mown salt marsh. J. Veg. Sci. 3, 247–252.

Beeftink, W.G., Daane, M.C., De Munck, W., Nieuwenhuize, J., 1978. Aspects of population dynamics in *Halimione portulacoides* communities. Vegetatio 36, 31–43.

Bonis, A., Bouzillé, J.B., Jigorel, A., Langlois, E., 2000. Sediment dynamics. Interaction between plants and sediments. Final report, work program PL 970655, European salt marshes modelling.

Bouchard, V., Digaire, F., Lefeuvre, J.C., Guillon, L.M., 1995. Progression des prés salés à l’ouest du Mont-Saint-Michel entre 1984 et 1994. Mappemonde 4, 28–34.

Chang, E.R., Carleton, T.J., Jefferies, R.L., 2001. Relationship between vegetation and soil seedbanks in an arctic coastal marsh. J. Ecol. 89, 367–384.

Dormann, C.F., Van Der Wal, R., Bakker, J.P., 2000. Competition and herbivory during salt marsh succession: the importance of forb growth strategy. J. Ecol. 88, 571–583.

Gounot, M., 1969. Méthode d’étude quantitative de la végétation. Masson et Cie, Paris.

Gray, A.J., Scott, R., 1977. Biological flora of the British isles: *Puccinellia maritima*. J. Ecol. 65, 699–716.

Guillon, L.M., 1980. Les moutons de pré-salés en baie du Mont-Saint-Michel. DAA, ENSAIA, Nancy.

Guillon, L.M., 1984. Les schorres de la baie du Mont-Saint-Michel: unités de végétation et facteurs du milieu. Report CEE, Environnement 608F (SD), Laboratoire d’évolution des systèmes naturels et modifiés, Rennes.

Handa, I.T., Harmsen, R., Jefferies, R.L., 2002. Patterns of vegetation change and the recovery potential of degraded areas in a coastal marsh system of Hudson Bay lowlands. J. Ecol. 90, 86–99.

Hutchings, M.J., Russell, P.J., 1989. The seed regeneration dynamics of an emergent salt marsh. J. Ecol. 77, 615–637.

Jefferies, R.L., 1977. Growth responses of coastal halophytes to inorganic nitrogen. J. Ecol. 65, 847–865.

Jefferies, R.L., Perkins, N., 1977. The effects on the vegetation of the additions of inorganic nutrients to salt marsh soils at Stiffkey, Norfolk. J. Ecol. 65, 867–882.

Jensen, A., 1985. The effect of cattle and sheep grazing on salt marsh vegetation at Skallingen, Denmark. Vegetatio 60, 37–48.

Kaye, J.P., Hart, S.C., 1997. Competition for nitrogen between plants and soil microorganisms. Trends Ecol. Evol. 12, 139–143.

Kiehl, K., Eischeid, I., Gettner, S., Walter, J., 1996. Impact of different sheep grazing intensities on salt marsh vegetation in northern Germany. J. Veg. Sci. 7, 99–106.

Kiehl, K., Esselink, P., Bakker, J.P., 1997. Nutrient limitation and plant species composition in temperate salt marshes. Oecologia 111, 325–330.

Leendertse, P., 1995. Impact of nutrient and heavy metals on salt marsh vegetation in the Wadden Sea. Thesis University of Amsterdam.

Lefeuvre, J.C., Bouchard, V., Feunteun, E., Grare, S., Lafaille, P., Radureau, A., 2000. European salt marshes diversity and functioning: the case study of the Mont Saint-Michel bay, France. Wetlands Ecol. Manage 8, 147–161.

Olff, H., de Leeuw, J., Bakker, J.P., Platerink, R.J., van Wijnen, H.J., de Munck, W., 1997. Vegetation succession and herbivory in a salt marsh: changes induced by sea level rise and silt deposition along an elevational gradient. J. Ecol. 85, 799–814.

Pigott, C.D., 1969. Influence of mineral nutrition on the zonation of flowering plants in coastal salt-marshes. In: Rorison, I.H., et al. (Eds.), Ecological Aspects of the Mineral Nutrition of Plants. Blackwell Scientific Publications, Oxford, pp. 25–35.

Ranwell, D.S., 1972. Ecology of salt marshes and sand dunes. Chapman, Hall, London.

Scholten, M., Blaauw, P.A., Stroetenga, M., Rozema, J., 1987. The impact of competitive interactions on the growth and distribution of plant species in salt marshes. In: Huiskes, A.H.L., Blom, C.W.P.M., Rozema, J. (Eds.), Vegetation Between Land and Sea. pp. 270–281.

Stewart, G.R., Lee, J.A., Orebamjo, T.O., 1972. Nitrogen metabolism of halophytes I. Nitrate reductase activity in *Suaeda maritima*. New Phytol. 72, 539–546.

Tessier, M., Gloaguen, J.C., Lefeuvre, J.C., 2000. Factors affecting the population dynamics of *Suaeda maritima* at initial stages of development. Plant Ecol. 147, 193–203.

Tessier, M., Gloaguen, J.C., Bouchard, V., 2002. The role of spatio-temporal heterogeneity in the establishment and maintenance of the annual *Suaeda maritima* in salt-marsh plant communities. J. Veg. Sci. 13, 115–122.

Tutin, T.G., Heywood, V.H., Burges, N.A., Valentine, D.H., Walters, S.M., Webb, D.A., 1964–1980. Flora Europea. Cambridge University Press, Cambridge.

Ungar, I.A., Woodel, S.R.J., 1996. Similarity of seed banks to aboveground vegetation in grazed and ungrazed salt marsh communities on the Gower peninsula, South Wales. Int. J. Plant Sci. 157, 746–749.

Ungar, I.A., 1998. Are biotic factors significant in influencing the distribution of halophytes in saline habitats? Bot. Rev. 64, 176–199.

Valiela, I., Teal, J.M., 1974. Nutrient limitation in salt marsh vegetation. In: Reimold, R.J., Queen, W.H. (Eds.), Ecology of Halophytes. Academic Press, New York, pp. 547–563.

Van Wijnen, H.J., Bakker, J.P., 2000. Annual nitrogen budget of a temperate coastal barrier salt-marsh system along a productivity gradient at low and high marsh elevation. Perspectives in Plant Ecology, Evolution and Systematics 3/2, 128–141.

Van Wijnen, H.J., Van Der Wal, R., Bakker, J.P., 1999. The impact of herbivores on nitrogen mineralization rate: consequences for salt-marsh succession. Oecologia 118, 225–231.

Van Wijnen, H.J., Bakker, J.P., 1997. Nitrogen accumulation and plant replacement in three salt marsh systems in the Wadden Sea. J. Coastal Conserv. 3, 19–26.

Van Wijnen, H.J., Bakker, J.P., 1999. Nitrogen and phosphorus limitation in a coastal barrier salt marsh: the implications for vegetation succession. J. Ecol. 87, 265–272.

Van Wijnen, H.J., Bakker, J.P., de Vries, Y., 1997. Twenty years of salt marsh succession on a Dutch coastal barrier island. J. Coastal Conserv. 3, 9–18.

Vivier, J.P., 1997. Influence du pâturage sur la disponibilité de l’azote pour l’exportation dans un marais salé (Baie du Mont-Saint-Michel). Thesis University of Rennes.