

EFFECTS OF SHEEP GRAZING ON SALT-MARSH PLANT COMMUNITIES
IN THE BAY OF SOMME (FRANCE)Antoine MEIRLAND^{1,2}, Audrey BOUVET², Hervé RYBARCZYK^{2,3},
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RÉSUMÉ.— *Effet du pâturage ovin sur les communautés végétales des marais salés de la baie de Somme (France).*— L'utilisation du pâturage par les animaux domestiques pour gérer les écosystèmes des marais salés est toujours débattue et demande plus d'investigations de terrain. L'effet du pâturage sur les communautés végétales a été étudié dans des marais salés de la Baie de Somme (France). Nous avons comparé les caractéristiques de la végétation entre deux lots de relevés pâturés et non pâturés. Les différences de composition spécifique ont été évaluées par des tests de permutations multiples (Multi-Response Permutation Procedures; MRPP). Nous avons utilisé une analyse des espèces indicatrices (ISA) pour identifier les espèces caractéristiques des zones pâturées et non pâturées et des courbes rangs-abondances pour décrire les structures des communautés. Les différences de richesse en espèces, de hauteur et de biovolume des plantes ont été évaluées par des tests de Mann-Whitney. Les MRPP ont montré que les compositions des communautés pâturées, dominées par *Puccinellia maritima* et *Festuca rubra* ssp. *litoralis*, et non pâturées, dominées par *Halimione portulacoides*, diffèrent significativement ($T = -60,37$; $A = 0,10$; $p < 0,0001$). Neuf espèces sont indicatrices des zones pâturées et quatre des zones non pâturées. Les communautés pâturées présentent une richesse spécifique plus élevée ($3,5 \pm 0,2$ espèces.m⁻²) que celles non pâturées ($2,9 \pm 0,1$ espèces.m⁻²; $p < 0,001$). Cette différence est notable dans des systèmes habituellement caractérisés par de faibles contrastes de richesse. Dans les relevés pâturés, la hauteur et le biovolume de végétation sont plus faibles et le recouvrement de la végétation plus élevé que dans les relevés non pâturés. Selon l'identité des espèces, les plantes perdent de 16,7 à 86,3% de leur hauteur sous pâturage ovin. Les espèces montrant la plus importante perte de hauteur (> 50%) sont principalement des halophytes pionnières et des Poacées. *Aster tripolium*, *Suaeda maritima* var. *maritima*, *Halimione portulacoides*, *Spergularia marina* sont particulièrement sensibles au pâturage et perdent plus de 90% de leur biovolume en présence des moutons. À travers des effets en cascade, le pâturage ovin réduit la hauteur de végétation, contrôle l'identité des espèces dominantes, limite les interactions compétitives pour la lumière entre espèces et, finalement, augmente la richesse spécifique. Nous recommandons donc un pâturage modéré et extensif pour la gestion des marais salés européens occupés par quelques espèces très dominantes. Finalement, nous avons classé les espèces selon leur degré d'abrutissement et leur valeur indicatrice de pâturage (ISA) pour fournir aux bergers un outil de terrain leur permettant d'évaluer l'impact des moutons sur les plantes des marais salés.

SUMMARY.— The use of domestic animal grazing to manage temperate salt-marsh ecosystems is still debated and requires further field investigations. The effects of sheep grazing on plant community were studied in the salt-marshes of the Bay of Somme (France). We compared vegetation characteristics between two sets of grazed and ungrazed 1m²-plots. We tested for differences in species composition using pair-wise Multi-Response Permutation Procedures (MRPP), used an Indicator Species Analysis (ISA) to distinguish

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species indicator of grazed and ungrazed areas and described community structures with species rank-abundance curves. Differences in species richness and plant height and biovolume were tested using Mann-Whitney tests. MRPP showed that plant community composition differed significantly between grazed plots, dominated by *Puccinellia maritima* and *Festuca rubra* ssp. *litoralis*, and ungrazed plots, dominated by *Halimione portulacoides* ($T = -60.37$; $A = 0.10$; $p < 0.0001$). Nine species were indicator of grazed areas and four of ungrazed areas. Grazed communities had higher species richness (3.5 ± 0.2 species.m⁻²) than ungrazed communities (2.9 ± 0.1 species.m⁻²; $p < 0.001$). This significant difference is noteworthy in salt-marsh systems usually characterized by low contrasts of species richness. In grazed plots, vegetation height and biovolume were lower but vegetation cover was higher than in ungrazed plots. According to the identity of the species, plants lost 16.7% to 86.3% of their height under grazing pressure. The species showing the highest decrease in height (> 50%) were mainly pioneer halophytes and grasses. *Aster tripolium*, *Suaeda maritima* var. *maritima*, *Halimione portulacoides*, *Spergularia marina* were heavily damaged or browsed and lost more than 90% of their biovolume in grazed area. Through cascading effects, sheep grazing reduces the vegetation height, controls the identity of dominant species, relaxes competitive interaction for light between species and, finally, positively influences plant species richness. We thus recommend a moderate and extensive sheep grazing to manage European salt-marshes dominated by few highly competitive plant species. Finally, we categorized species according to their height loss percentage under grazing and their indicator value from ISA to provide a field tool to help the shepherds to estimate the impact of grazing on salt-marsh plants.

The diversity of salt-marsh vegetation in Western Europe has been largely shaped by a long history of natural and human-managed grazing (Nieuwhof, 2006; Britton *et al.*, 2008). Before human settlement, the presence of large herbivores (deer, aurochs, and horses) in tidal areas was shown by archaeological researches (Allen, 1997). Today, in the human-free and in the less human-disturbed salt-marshes, a form of natural (or at least spontaneous) grazing is still ongoing and is mainly maintained by Anatidae birds (Smith III & Odum, 1981; Fox & Kahlert, 2003). Other animals, rabbit (Stapf, 1907), hare (Kuijper *et al.*, 2008), muskrat (Lynch *et al.*, 1947), nutria (Grace & Pugsek, 1997; Evers *et al.*, 1998), wild guinea pig (Alberti *et al.*, 2011), wild boar (Grace & Pugsek, 1997) and feral horse (Turner, 1987) can contribute to coastal marsh grazing as well. This natural or spontaneous grazing is not the most common form of grazing in the present day estuaries. Most of the estuarine ecosystems are now largely patterned by human activities (Chabrierie *et al.*, 2001; Esselink *et al.*, 2002) and domestic sheep and cattle flocks have long since replaced the ancient natural grazers and, probably, their functions (Lefeuvre *et al.*, 2000; Bouchard *et al.*, 2003; Bakker *et al.*, 2008; Olsen *et al.*, 2011). Therefore, the human-controlled grazing has become a main driving force of plant diversity in salt-marsh.

A question then arises: is it good or bad to recommend “artificial” sheep or cattle grazing to manage, conserve or restore “natural” salt-marshes? In other words, should we submit estuarine ecosystems primarily bottom-up controlled by natural physical and chemical factors (altitude, salt, flooding, nutrients) (Sala *et al.*, 2008) to a top-down control of vegetation biomass and diversity by domestic animals, as it is the case in other terrestrial herbaceous systems (Denyer *et al.*, 2010)?

There is substantial discrepancy among salt-marsh studies about the effects of grazing on species diversity. Contrasted effects of grazing have been reported in the literature (Olff & Ritchie, 1998). The existence of either positive or negative relationships between grazing and plant species diversity in salt-marsh depends on a great variety of parameters such as the observation scale (Dupré & Diekmann, 2001), the study site or the vegetation succession stage (Dupré & Diekmann, 2001; Milotić *et al.*, 2010), the identity of herbivores (Kuijper *et al.*, 2008), the intensity of grazing (Bouchard *et al.*, 2003), the duration (Tessier *et al.*, 2003) and the seasonality of grazing (Bullock *et al.*, 2001; Tessier *et al.*, 2003). Although these various environmental contexts exist in the salt-marshes, a continuous grazing is often necessary for the survival of halophyte species (Jensen, 1985) and most of the studies revealed a positive effect of sheep, cattle and horse grazing on plant species richness (Berg *et al.*, 1997; Loucougaray *et al.*, 2004; Amiaud *et al.*, 2008). Therefore, grazing is commonly considered as one of the most efficient restoration and management tools in salt-marsh (Bouchard *et al.*, 2003; Wolters *et al.*, 2005).

However, when too heavy, grazing can lead to salt-marsh ecosystem alteration and plant species diversity decrease. This loss in plant diversity has been observed in salt-marshes intensively grazed by sheep (Kiehl *et al.*, 1996; Milotić *et al.*, 2010) and geese (Handa & Jefferies, 2000; McLaren & Jefferies, 2004; Buckeridge & Jefferies, 2007). Decades of intensive grazing can reduce plant diversity via the deterioration of sediments and soil processes or by producing large areas of monotonous vegetation dominated by grasses (Kiehl *et al.*, 1996). In this case, the cessation of sheep grazing is sometimes recommended for nature conservation (Kiehl *et al.*, 1996).

The mechanisms through which grazing influences plant species richness and composition in salt-marsh are diversified.

A first main direct effect of grazing on vegetation is the control of the above-ground biomass level and the vegetation height (Milchunas & Lauenroth, 1993; Evers *et al.*, 1998): the canopy height decreases with increasing stocking rate (Andresen *et al.*, 1990). Cattle grazing is known to reduce the canopy height and increase the amount of light reaching the soil, enabling seedlings of salt-marsh species to survive (Baker, 1992) and adult plants to spread (Bakker *et al.*, 1985). At the opposite, the abandonment of grazing generally results in a development of tall grasses and herbs (Ranwell, 1961) and an accumulation of litter (WallisDeVries *et al.*, 1998), closing the canopy and excluding many low-stature species. In this way, grazing is expected to increase species richness by maintaining a low vegetation height or biomass (Grace & Pugsek, 1997).

By controlling the vegetation height and the level of above-ground biomass, the grazers also modify the competitive relationships and the dominance of the so called ‘core’ species (Collins *et al.*, 1993). The identity and dominance of core species determine the number of ‘satellite’ species which are the principal contributors of the species richness in the community. A competitive hierarchy exists between core species, according to their height and the space they are able to pre-empt (Bockelmann & Neuhaus, 1999). The exclusion of large herbivores conducted to the dominance of salt-marsh plant communities by a small set of tall herbs and/or highly competitive species such as *Elymus athericus* (Andresen *et al.*, 1990; Van Wijnen *et al.*, 1997), *Elymus repens* (Bakker *et al.*, 1997; Amiaud *et al.*, 2008), *Phragmites australis* (Siira, 1970; Kleyer *et al.*, 2003) or *Halimione portulacoides* (Jensen, 1985; Kleyer *et al.*, 2003; Tessier *et al.*, 2003).

All these species are not equivalent to the herbivore ‘point of view’ (Ginane & Dumont, 2010). The selective herbivory is also another way of driving species competition and community structure (Furbish & Albano, 1994). The herbivores select the species they eat according to their morphological traits or their palatability (Bullock *et al.*, 2001). Thus, species can maintain in grazed area for various reasons: for example, grasses tolerate a biomass reduction and develop vegetatively whilst some other species are sensitive to biomass reduction but survive thanks to their toxicity or low palatability (Dormann & Van Der Wal, 2000; Cingolani *et al.*, 2005).

A second important grazing component driving species diversity is the trampling effect. Trampling creates small patches of bare soil within the vegetation cover (Milton *et al.*, 1997; Dhillon, 1999). These gaps in the vegetation are suitable sites for germinations (Hillier, 1990; Rusch & Fernandez-Palacios, 1995) and enable species turnover in the communities (Grubb, 1977; Rusch & Van der Maarel, 1992). Indeed, the number of emerging seedlings is positively related to the percentage of bare soil created by herbivores (Bakker & de Vries, 1992). Nevertheless, this trampling effect, when too heavy, can also reduce the number of species sensitive to soil disturbances (Andresen *et al.*, 1990). Indirect effects of trampling on vegetation through a modification of soil conditions are likely to occur too. Several studies reported that in intensively cattle grazed areas, the soil salinity increases, as a consequence of trampling and low vegetation cover in spring (Esselink *et al.*, 2002; Bonis *et al.*, 2005). This indirect effect of grazing on vegetation could promote the halophytic species.

A third crucial function of herbivores in salt-marsh is their role in seed dispersal. Large herbivores (cattle) as well as small herbivores (hares, geese) play an important role in structuring salt-marsh plant communities via endozoochorous seed dispersal (Amiaud *et al.*, 2000;

Chang *et al.*, 2005; Bakker *et al.*, 2008). Although studies dealing with seed dispersal by sheep in salt-marsh sites are lacking, sheep is probably an important vector of seeds through endozoochory (Pakeman & Small, 2009) and ectozoochory (Tackenberg *et al.*, 2006). Consequently, we can expect a higher diversity in grazed areas receiving more endozoochorous seeds than ungrazed sites.

Compared to the other French estuaries, the Bay of Somme (North-western France) is a medium-sized estuary that has been relatively preserved from the development of industrial areas and harbour facilities. This low industrial pressure in the Bay of Somme is an opportunity to study plant community processes in semi-natural conditions. Our aim was to evaluate the effects of sheep grazing on salt marsh plant communities in the Bay of Somme and to compare these effects to those reported in the literature. We hypothesize that sheep grazing reduces the canopy height and the dominance of core species in the community. Consequently, domestic herbivores increase light availability for numerous other species, changing community composition, promoting rosette, low-stature species and grazing-tolerant grasses and, *in fine*, increasing local species richness. We compared community composition, species richness as well as height and biovolume of plant species between two sets of grazed and ungrazed plots to assess the effect of grazing at both community and plant scales. The effect of biomass removal by grazing at the species scale was discussed and used to better understand the mechanisms of species coexistence occurring at the community scale.

MATERIALS & METHODS

STUDY SITE

The Bay of Somme (50.20°N; 1.62°E) in the Eastern Channel is the second largest estuarine system of the North of France. This macrotidal estuary has a tidal range of 11 m and receives low fresh water input mainly from the Somme River (30 m³.s⁻¹). The salt-marsh vegetation of the Bay of Somme covers 1930 ha of which 1150 ha are managed as extensive pasture under the control of the French state's administration. About 4670 sheep are free-ranging or are under the guidance of a shepherd. On average, the grazing pressure is estimated at 4 sheep.ha⁻¹ but it highly varies in space and time. Between 15 Mar and 1 Dec, a maximum of 5 sheep per hectare is allowed by law in the bay. The sheep density is restricted to 2 and 1.33 sheep.ha⁻¹ in December and between 1 Jan and 15 Mar, respectively. During the highest tides (tidal coefficient > 100), the flocks are moved on continental grasslands near the bay. Nightly, sheep are parked in the upper salt-marsh. The high density of dendritic channels has created a labyrinth of areas more or less accessible for sheep. Consequently, the vegetation of the bay is a complex mosaic of grazed and ungrazed areas in which sheep are sometimes lost after the tides.

SAMPLING

We disposed two sets of 135 and 158 1m²-plots respectively in the mosaic of grazed and ungrazed areas of the Somme bay. Plots were spaced by a minimum of 30 m distance to prevent from spatial and biological dependence between them (Chabrerie & Alard, 2005). On each plot, we estimated the cover of vascular plant species as well as total vegetation cover, height, and biovolume (biovolume = vegetation height x vegetation cover) from July to August 2010. We visited plots with late flowering species (*Salicornia* and *Atriplex* genus) a second time in September 2010 to identify them. Nomenclature was in accordance with Lambinon *et al.* (2004) and Lahondère (2004) for the genus *Salicornia*. We also calculated the mean height of each species by measuring 5 individuals randomly selected on each 1m²-plot. After what we calculated the biovolume of each species on each plot (species biovolume = mean species height x species cover) so as to provide an estimator of space occupancy and competition performance of species (Van der Maarel, 2007). As the number of faeces increased linearly with stocking rates (Tadey & Farji-Brener, 2007), we counted number of sheep faeces on sampling plots to quantify grazing intensity.

ANALYSES

We tested for differences in species composition between grazed and ungrazed plots by means of pairwise multi-response permutation procedures (MRPP) using the relative Euclidean distance measure (Zimmerman *et al.*, 1985). Species rank-abundance curves (Ludwig & Reynolds, 1988), were used to examine the structures of grazed and ungrazed communities. Species composition difference between grazed and ungrazed communities was described using indicator species analysis (ISA) (Dufrene & Legendre, 1997) including a Monte Carlo test of significance based on 1 000 randomizations ($p < 0.05$). MRPP and ISA were carried out using PC-ORD® v. 4.25 software (McCune & Mefford, 1999).

We conducted comparisons of vegetation species richness, height and biovolume between grazed and ungrazed plots using Mann-Whitney tests. To search whether an increasing grazing intensity was associated with changes in

vegetation physiognomy, we conducted Spearman rank correlations ($p < 0.05$) between number of sheep faeces and vegetation height and biovolume within the subset of grazed plots.

To assess the effect of sheep grazing at the plant and population scales, we compared the plant height and population biovolume of each species between grazed and ungrazed plots using Mann-Whitney tests. All univariate analyses were performed using SPSS v. 17.0 (IBM Corp., Somers, NY, USA).

We finally transformed the species indicator values (IV) of Dufrene and Legendre (1997) into a continuous grazing index by attributing a negative IV to indicator species of ungrazed plots and a positive IV to indicator species of grazed plots, more its transformed IV was high. Transformed IV and mean height loss by plant species between grazed and ungrazed plots were bi-plotted in order to group species in four categories according to their sensitivity to grazing: (1) species promoted by grazing (indicator species of grazed areas) but slightly browsed by sheep (low height reduction after grazing indicating a low palatability or an adaptation to escape defoliation); (2) species promoted by grazing and highly browsed (high height reduction after grazing indicating a high palatability); (3) indicator species of ungrazed areas, slightly browsed; (4) indicator species of ungrazed areas, highly browsed (species suffering from grazing). The species totally absent from grazed or from ungrazed sites were not plotted as it was not possible to calculate their height loss between the two sets of plot.

RESULTS

COMMUNITY COMPOSITION

MRPP showed that plant community composition differed significantly between grazed and ungrazed plots ($T = -60.37$; $A = 0.10$; $p < 0.0001$). The two species rank-abundance curves showed similar patterns (Fig. 1) and indicated that both grazed and ungrazed communities were dominated by few species. However, there was a shift in the identity of dominant species between grazed and ungrazed plots. The shrubby halophyte *Halimione portulacoides*, which dominates ungrazed areas, was replaced by two small halophyte grasses (*Puccinellia maritima* and *Festuca rubra* ssp. *litoralis*) in grazed areas. *Elymus athericus* and *Atriplex prostrata* were abundant in the two sets of plot. The number of species preferentially distributed in grazed plots was higher than the number of indicator species of ungrazed plots (ISA; Tab. I). Species characteristic of grazed areas were mainly grasses (*Puccinellia maritima*, *Festuca rubra* ssp. *litoralis*, *Agrostis stolonifera*, *Puccinellia* sp.), rosette species (*Limonium vulgare*, *Plantago maritima*, *Triglochin maritima*) and annual and perennial low-stature, prostrated plant types (*Spergularia media*, *Glaux maritima*). The two species *Glaux maritima* and *Limonium vulgare* were totally absent from ungrazed plots. Indicator species of ungrazed plots were pioneer halophytes (*Spartina townsendii* var. *anglica*, *Suaeda maritima* var. *maritima*, *Bolboschoenus maritimus*, *Aster tripolium*) and *Halimione portulacoides*, the dominant species of the Bay of Somme.

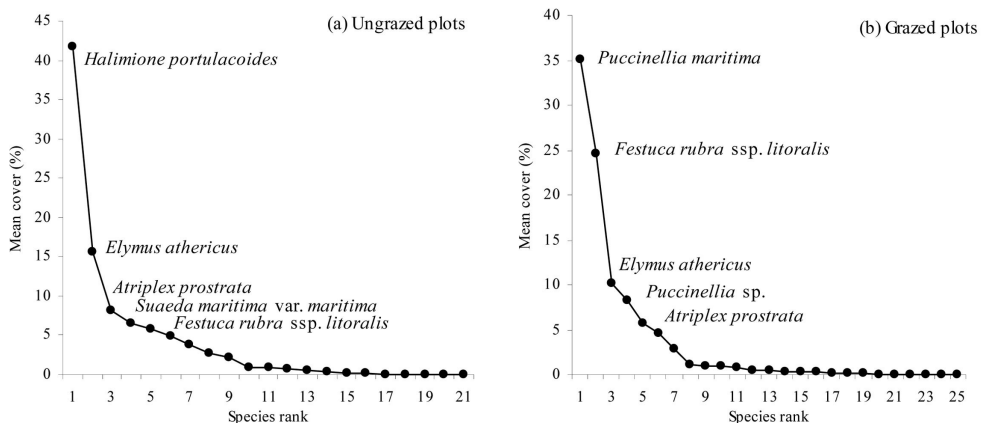


Figure 1.— Species rank-abundance curves in (a) ungrazed and (b) grazed plots. Only species with mean cover > 5% are shown.

TABLE I

Results of indicator species analysis (ISA) conducted on ungrazed and grazed plots. ^a: only species with p -values < 0.05 are shown. ^b: p -values from Monte Carlo tests are based on the proportion of randomized trials with expected IV $>$ observed IV. Species are ranked according their indicator value

Indicator species ^a	Observed indicator value (IV)	p -value ^b
Ungrazed plots (N=158)		
<i>Halimione portulacoides</i>	47.1	0.001
<i>Suaeda maritima</i> var. <i>maritima</i>	23.7	0.001
<i>Aster tripolium</i>	22.5	0.015
<i>Spartina townsendii</i> var. <i>anglica</i>	8.3	0.023
<i>Bolboschoenus maritimus</i>	7.5	0.028
Grazed plots (N=135)		
<i>Puccinellia maritima</i>	43.4	0.001
<i>Festuca rubra</i> ssp. <i>litoralis</i>	31.8	0.001
<i>Glaux maritima</i>	19.3	0.001
<i>Agrostis stolonifera</i>	14.7	0.001
<i>Spergularia media</i>	13.8	0.001
<i>Puccinellia</i> sp.	10.7	0.001
<i>Limonium vulgare</i>	10.4	0.001
<i>Plantago maritima</i>	6.7	0.001
<i>Triglochin maritima</i>	7.4	0.002

SPECIES RICHNESS AND VEGETATION PHYSIOGNOMY

Grazed plots showed lower vegetation height and biovolume but higher species richness and vegetation cover than ungrazed plots (Tab. II). The species pool hosted by the grazed areas is slightly higher ($n = 25$) than the species pool of the ungrazed areas ($n = 21$). In grazed plots, the height and volume of vegetation were reduced by 51.7% and 50.8%, respectively. Within grazed areas, an increasing grazing intensity estimated by sheep faeces density was associated with a decreasing vegetation height ($R = -0.470$; $p < 0.001$) and biovolume ($R = -0.467$; $p < 0.001$).

TABLE II

Mean (\pm standard error) values of species richness, vegetation cover, height and biovolume on grazed and ungrazed plots. N is the number of plots. Z is the value of the Mann-Whitney's test

	Ungrazed			Grazed			Total			Mann-Whitney test	
	N	Mean	S.E.	N	Mean	S.E.	N	Mean	S.E.	Z	p -value
Species richness	158	2.4	0.1	135	3.5	0.2	293	2.9	0.1	-5.714	<0.001
Vegetation cover (%)	158	95.4	1.3	135	97.6	0.5	293	96.4	0.7	-3.651	<0.001
Vegetation height (cm)	158	66.9	1.9	135	32.3	1.9	293	51.0	1.7	-10.584	<0.001
Biovolume ($m^3 \cdot m^{-2}$)	158	0.65	0.02	135	0.32	0.02	293	0.49	0.02	-10.203	<0.001

PLANT HEIGHT AND BIOVOLUME

Thirteen species showed significant differences in height between grazed and ungrazed plots (Tab. III). The differences in plant height between grazed and ungrazed plots varied from 1 cm to 63 cm. Plants lost 16.7 to 86.3% of their height between grazed and ungrazed plots. The species showing the highest decrease in height ($> 50\%$) were mainly pioneer halophytes (*Aster*

tripolium, *Salicornia* sp., *Suaeda maritima* var. *maritima*, *Halimione portulacoides*, *Atriplex prostrata*) and grasses indicator of grazing (*Puccinellia maritima*, *Agrostis stolonifera*).

TABLE III

Mean (\pm standard error) values of plant height on grazed and ungrazed plots. *N* is the number of plots where a given species was recorded. *Z* is the value of the Mann-Whitney's test. ^a: DELTA height in cm = mean height on grazed plots - mean height on ungrazed plots. ^b: DELTA height in % = 100 * (mean height on ungrazed plots - mean height on grazed plots) / mean height on ungrazed plots. Species are ranked according to the difference in height (DELTA height in %) between the two sets of plots

Species	Ungrazed			Grazed			Total			DELTA height		Mann-Whitney test	
	<i>N</i>	Mean	S.E.	<i>N</i>	Mean	S.E.	<i>N</i>	Mean	S.E.	cm ^a	% ^b	<i>Z</i>	<i>p</i>
<i>Aster tripolium</i>	40	56.3	4.1	30	13.0	1.3	70	37.7	3.5	-43.4	-77.0	-7.004	<0.001
<i>Puccinellia</i> sp.	3	45.0	17.7	14	12.2	2.5	17	18.0	4.6	-32.8	-72.9	-2.403	0.016
<i>Puccinellia maritima</i>	21	43.3	4.4	66	12.3	1.2	87	19.8	2.0	-30.9	-71.5	-6.072	<0.001
<i>Artemisia maritima</i>	5	37.8	4.7	12	11.9	2.8	17	19.5	3.7	-25.9	-68.5	-2.957	0.003
<i>Salicornia</i> sp.	15	47.1	3.7	7	14.9	2.1	22	36.8	4.2	-32.1	-68.3	-3.491	<0.001
<i>Spergularia media</i>	2	29.0	2.0	19	9.2	0.8	21	11.1	1.5	-19.8	-68.1	-2.291	0.022
<i>Suaeda maritima</i> var. <i>maritima</i>	38	47.3	2.6	21	17.8	2.0	59	36.8	2.6	-29.5	-62.4	-5.963	<0.001
<i>Agrostis stolonifera</i>	5	49.6	10.7	24	19.8	2.1	29	25.0	3.2	-29.8	-60.0	-2.604	0.009
<i>Halimione portulacoides</i>	72	60.9	1.8	15	24.9	4.1	87	54.7	2.2	-36.0	-59.1	-5.469	<0.001
<i>Atriplex prostrata</i>	60	55.0	3.4	84	23.8	1.8	144	36.8	2.2	-31.2	-56.8	-7.561	<0.001
<i>Bolboschoenus maritimus</i>	13	77.1	5.2	4	44.3	6.1	17	69.4	5.4	-32.8	-42.6	-2.726	0.006
<i>Festuca rubra</i> ssp. <i>litoralis</i>	26	36.8	3.7	51	24.2	2.0	77	28.4	1.9	-12.6	-34.2	-3.298	0.001
<i>Elymus athericus</i>	43	71.7	2.6	45	49.9	3.0	88	60.6	2.3	-21.9	-30.5	-4.831	<0.001
<i>Spergularia marina</i>	2	14.0	6.0	9	10.0	1.4	11	10.7	1.5	-4.0	-28.6	-0.715	0.474
<i>Spartina townsendii</i> var. <i>anglica</i>	14	63.5	7.5	4	49.3	9.8	18	60.3	6.2	-14.3	-22.4	-0.797	0.426
<i>Cochlearia anglica</i>	2	6.0	1.0	2	5.0	1.0	4	5.5	0.6	-1.0	-16.7	-0.775	0.439
Species not frequent enough to be tested													
<i>Salicornia fragilis</i>	5	38.2	7.2	-	-	-	5	38.2	7.2	-	-	-	-
<i>Cirsium arvense</i>	4	73.3	4.7	1	10.0	-	5	60.6	13.2	-63.3	-86.3	-	-
<i>Elymus repens</i>	3	46.3	5.8	-	-	-	3	46.3	5.8	-	-	-	-
<i>Calystegia sepium</i>	1	75.0	-	-	-	-	1	75.0	-	-	-	-	-
<i>Sonchus arvensis</i>	1	77.0	-	-	-	-	1	77.0	-	-	-	-	-
<i>Glaux maritima</i>	-	-	-	26	7.2	1.0	26	7.2	1.0	-	-	-	-
<i>Limonium vulgare</i>	-	-	-	14	19.4	2.1	14	19.4	2.1	-	-	-	-
<i>Plantago maritima</i>	-	-	-	9	6.7	1.2	9	6.7	1.2	-	-	-	-
<i>Triglochin maritima</i>	-	-	-	9	10.9	1.4	9	10.9	1.4	-	-	-	-
<i>Lolium perenne</i>	-	-	-	3	40.3	15.6	3	40.3	15.6	-	-	-	-
<i>Spergularia</i> sp.	-	-	-	2	5.3	3.8	2	5.3	3.8	-	-	-	-
<i>Alopecurus geniculatus</i>	-	-	-	1	18.0	-	1	18.0	-	-	-	-	-
<i>Atriplex littoralis</i>	-	-	-	1	4.0	-	1	4.0	-	-	-	-	-

Only six species showed a significant decrease of their biovolume between grazed and ungrazed plots (Tab. IV). Among them *Aster tripolium*, *Suaeda maritima* var. *maritima*, *Halimione portulacoides*, *Spergularia marina* lost more than 90% of their biovolume.

TABLE IV

Mean (\pm standard error) values of plant biovolume ($\text{m}^3 \cdot \text{m}^{-2}$) on grazed and ungrazed plots. N is the number of plots where a given species was recorded. Z is the value of the Mann-Whitney's test. ^a: DELTA biovolume in $\text{m}^3 \cdot \text{m}^{-2}$ = mean biovolume on grazed plots - mean biovolume on ungrazed plots. ^b: DELTA biovolume in % = $100 * (\text{mean biovolume on ungrazed plots} - \text{mean biovolume on grazed plots}) / \text{mean biovolume on ungrazed plots}$. Species are ranked according to the difference in biovolume (DELTA biovolume in %) between the two sets of plots

Species	Ungrazed			Grazed			Total			DELTA biovolume		Mann-Whitney test	
	N	Mean	S.E.	N	Mean	S.E.	N	Mean	S.E.	$\text{m}^3 \cdot \text{m}^{-2} \text{ }^a$	% ^b	Z	p
<i>Aster tripolium</i>	40	0.162	0.047	30	0.006	0.002	70	0.095	0.028	-0.16	-96.1	-4.747	<0.001
<i>Suaeda maritima</i> var. <i>maritima</i>	38	0.136	0.030	21	0.006	0.002	59	0.089	0.021	-0.13	-95.8	-3.166	0.002
<i>Halimione portulacoides</i>	72	0.554	0.027	15	0.039	0.029	87	0.465	0.031	-0.52	-93.0	-5.507	<0.001
<i>Spergularia marina</i>	2	0.008	0.000	9	0.001	0.000	11	0.002	0.001	-0.01	-90.7	-2.121	0.034
<i>Spartina townsendii</i> var. <i>anglica</i>	14	0.256	0.090	4	0.024	0.005	18	0.205	0.073	-0.23	-90.7	-0.850	0.396
<i>Bolboschoenus maritimus</i>	13	0.246	0.088	4	0.041	0.036	17	0.198	0.071	-0.21	-83.4	-1.019	0.308
<i>Artemisia maritima</i>	5	0.074	0.021	12	0.014	0.008	17	0.031	0.010	-0.06	-81.3	-1.792	0.073
<i>Atriplex prostrata</i>	60	0.154	0.036	84	0.036	0.009	144	0.085	0.017	-0.12	-76.5	-4.950	<0.001
<i>Salicornia</i> sp.	15	0.032	0.017	7	0.010	0.009	22	0.025	0.012	-0.02	-69.2	-1.022	0.307
<i>Spergularia media</i>	2	0.004	0.002	19	0.001	0.001	21	0.002	0.001	0.00	-66.7	-1.558	0.119
<i>Elymus athericus</i>	43	0.397	0.042	45	0.161	0.029	88	0.276	0.028	-0.24	-59.4	-4.462	<0.001
<i>Cochlearia anglica</i>	2	0.001	0.000	2	0.000	0.000	4	0.001	0.000	0.00	-57.1	-1.549	0.121
<i>Agrostis stolonifera</i>	5	0.114	0.074	24	0.051	0.012	29	0.062	0.016	-0.06	-55.2	-0.635	0.525
<i>Puccinellia maritima</i>	21	0.150	0.047	65	0.081	0.009	86	0.098	0.014	-0.07	-46.1	-0.814	0.416
<i>Puccinellia</i> sp.	3	0.086	0.057	14	0.078	0.007	17	0.079	0.010	-0.01	-9.6	-0.693	0.488
<i>Festuca rubra</i> ssp. <i>littoralis</i>	26	0.154	0.037	51	0.156	0.015	77	0.155	0.016	0.00	1.0	-1.330	0.183
Species not frequent enough to be tested													
<i>Salicornia fragilis</i>	5	0.011	0.009	-	-	-	5	0.011	0.009	-	-	-	-
<i>Cirsium arvense</i>	4	0.082	0.033	1	0.000	-	5	0.066	0.030	-0.08	-99.4	-	-
<i>Elymus repens</i>	3	0.251	0.165	-	-	-	3	0.251	0.165	-	-	-	-
<i>Calystegia sepium</i>	1	0.038	-	-	-	-	1	0.038	-	-	-	-	-
<i>Sonchus arvensis</i>	1	0.039	-	-	-	-	1	0.039	-	-	-	-	-
<i>Glaux maritima</i>	-	-	-	26	0.005	0.002	26	0.005	0.002	-	-	-	-
<i>Limonium vulgare</i>	-	-	-	14	0.063	0.020	14	0.063	0.020	-	-	-	-
<i>Plantago maritima</i>	-	-	-	9	0.002	0.001	9	0.002	0.001	-	-	-	-
<i>Triglochin maritima</i>	-	-	-	9	0.007	0.006	9	0.007	0.006	-	-	-	-
<i>Lolium perenne</i>	-	-	-	3	0.088	0.079	3	0.088	0.079	-	-	-	-
<i>Spergularia</i> sp.	-	-	-	2	0.000	0.000	2	0.000	0.000	-	-	-	-
<i>Alopecurus geniculatus</i>	-	-	-	1	0.002	-	1	0.002	-	-	-	-	-
<i>Atriplex littoralis</i>	-	-	-	1	0.001	-	1	0.001	-	-	-	-	-

GRAZING AND PLANT STRATEGIES

Figure 2 shows that *Halimione portulacoides*, and to a lesser degree *Aster tripolium* and *Suaeda maritima*, were clearly disadvantaged by grazing both because of a high defoliation pressure and a low occupancy of grazed plots. *Puccinellia* species and *Agrostis stolonifera* were intensively eaten by sheep (high height loss) but were favoured by the presence of grazer. *Festuca rubra* ssp. *littoralis* was present on both grazed and ungrazed plots (see Fig. 1)

but became dominant under grazing. This fescue, favoured by grazing (Tab. I), lost 34.2% in height (Tab. III) but gained 1% in biovolume on grazed plots (Tab. IV), indicating a trade-off between the loss of biomass and the gain of cover.

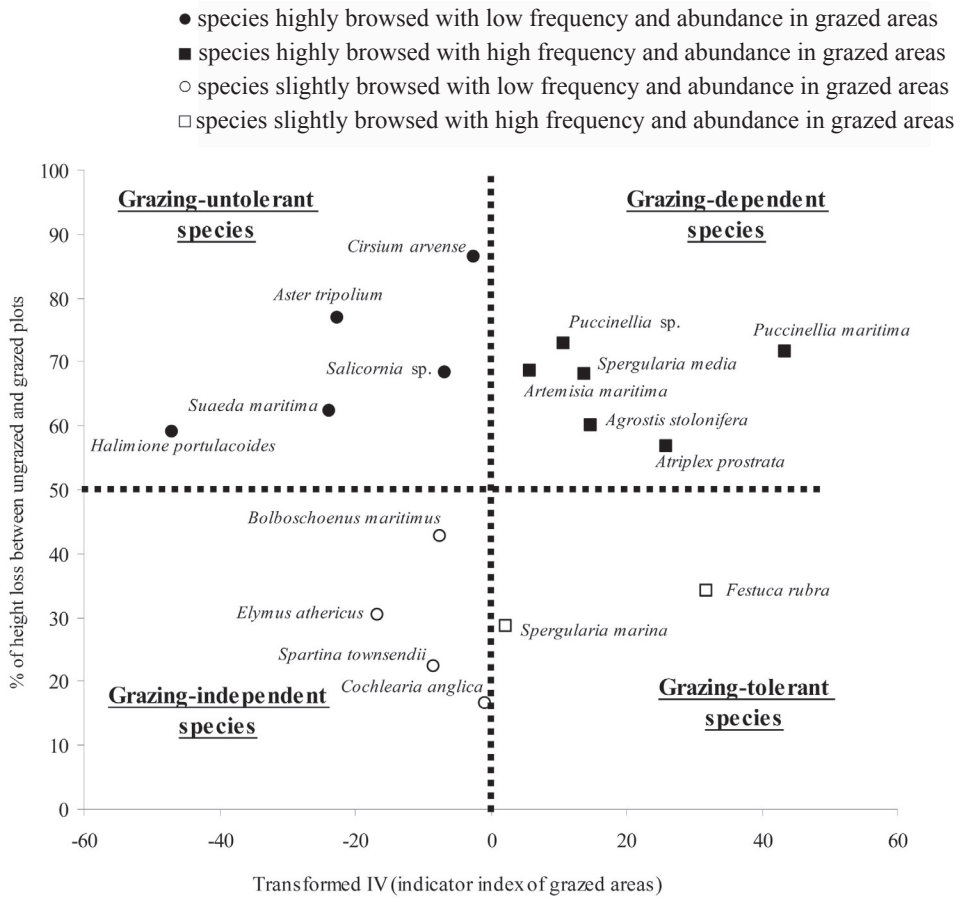


Figure 2.- Species grouped in four classes according to the proportion of plant browsed (i.e. their palatability) between ungrazed and grazed plots and their grazing indicator value (IV). Transformed IV: indicator value (IV, see Table I) of Dufrêne & Legendre (1997) transformed into a continuous grazing index. We attributed a negative IV for indicator species of ungrazed plots. Species exclusively present in ungrazed or in grazed plots were excluded, as it was not possible to calculate height differences between the two sets of plot.

DISCUSSION

GRAZING AND SPECIES COEXISTENCE

Our results show that sheep grazing primarily reduces the vegetation height and biovolume (see Tab. II). This reduction in vegetation height and biovolume increases with the intensity of grazing. It corroborates previous works highlighting the control of the community height or biomass by herbivores (Bakker & de Vries, 1992; Milchunas & Lauenroth, 1993). Concomitantly, sheep grazing increases species richness at the bay scale, i.e. at the landscape scale,

as there are more indicator species of grazed than of ungrazed areas (see the ISA). *A fortiori*, only 4 species (including 3 common ruderal generalist species and 1 halophyte) are exclusively present in ungrazed areas, whilst 8 species (including 6 halophytes) were observed solely in grazed areas (see Tab. III & IV). At the community scale, i.e. on the plots, sheep grazing also increases mean local species richness. We interpret this higher species richness as a major consequence of a low light interception by aerial biomass in grazed area (Bakker & de Vries, 1992). Competitive interactions between plants for light are relaxed by herbivore consumption (Olf & Ritchie, 1998) and, thus, more species are less light-limited and can coexist within small plots. At the opposite, the low amount of light reaching the soil in the ungrazed tall herb sites might be the limiting factor for species establishment, especially for halophytes suffering from light reduction during the first months of growth (Bakker *et al.*, 1985).

Under grazing pressure, plants probably shift from competing for light to competing for soil nutrients (Olf & Ritchie, 1998). In our study site, the number of faecal pellet fragments varied from 0 to about 200 per m² indicating a high variability of sheep activity between 1 m²-plots. As nitrogen released from urine deposition and faeces decomposition is a limiting factor for plant growth (Tessier *et al.*, 2003), there is a high spatial variability in resource supply between plots. This small scale heterogeneity in nutrient availability could have enhanced regeneration niche, niche partitioning and the coexistence of more plant species (Olf & Ritchie, 1998) in grazed sites. The presence of faeces fragments is also an indicator of seed input and species flux through endozoochory (Bakker *et al.*, 2008) and contributes to explain the higher species richness in grazed sites, probably less dispersal limited.

Results also show that vegetation cover slightly (but significantly) increases from ungrazed to grazed areas (Tab. II). Most studies show the opposite, i.e. an increase in bare soil cover in grazed sites (Jensen, 1985; Naeth *et al.*, 1991). In our study, the lower bare soil cover in grazed area didn't seem to affect species richness, probably because the amount of bare soil was higher than seemed necessary for germination and survival as suggested by Bakker & de Vries (1992). The low bare soil cover in our grazed sites can be explained by the clonal growth of the two dominant grasses, *Puccinellia maritima* and *Festuca rubra* ssp. *litoralis* (Hubbard, 1984), that quickly close the canopy gaps after sheep trampling. In grazed areas, space and resources are probably quickly and efficiently used by higher diversity of plant type (rosette, prostrate, annuals, guerrilla species). In the ungrazed mono- or pauci-specific communities of *Halimione portulacoides*, larger canopy gaps exist but no or very few species are able to establish in them. As salt-marshes are characterized by species-poor seed banks (Shumway & Bertness, 1992) and as seed rain is mainly an outcome of the local surrounding vegetation (Jensen, 1998), the stimulation of germination from seed bank and seed rain by canopy openings within the dense populations of *Halimione portulacoides* is probably not efficient enough to promote new seedling emergences and species establishments (Jensen, 1998). Consequently, these canopy gaps remain unused by other species and are finally closed by the sole dominating species.

The mechanisms behind the shift in community composition shown by the MRPP from ungrazed to grazed sites can be better understood by examining species rank-abundance curves and indicator species analysis (ISA). The core and tall forb, *Halimione portulacoides* typical of ungrazed areas, loses 93% of its biovolume in grazed areas and is replaced by the two short grasses, *Puccinellia maritima*, *Festuca rubra* ssp. *litoralis*, and numerous other low-abundance 'satellite' species. Therefore, sheep promote species richness by direct consumption of the dominant species and indirect modification of competitive interactions. The pattern of replacement of *Halimione portulacoides* by *Puccinellia maritima* is consistent with that observed in numerous west-European salt-marshes (Tessier *et al.*, 2003). It is partly due to the fact that tall species lose more biomass and become less dominant than prostrate species (Olf & Ritchie, 1998). In the Somme bay, sheep break large amounts of stems and plant fragments to create pathways and progress within the dense matrix of this tall forb (maximum high of *Halimione portulacoides*: 99 cm). As *Halimione portulacoides* is very sensitive to this mechanical damage (Jensen, 1998), free-ranging flocks of sheep should be a main factor influencing the equilibrium between *Halimione* and *Puccinellia* patches within the vegetation mosaic.

GRAZING, BIOMASS LOSS AND PLANT STRATEGIES

Although the totality of the species experienced a decrease in height and biovolume (except *Festuca rubra* ssp. *litoralis*) from ungrazed to grazed areas, the magnitude of plant material loss considerably varies between species (see Tab. III & IV) and reveals a gradient of plant strategies (see Fig. 2) ranging species from well-adapted to unadapted to herbivory.

A first group of plants, shown in Figure 2, is strongly promoted by grazing (indicator species of grazed plots with high frequency and abundance under a high herbivore pressure). These species generally cannot cope with the competition of tall herbs and disappear with the spread of *Halimione portulacoides* populations. In this way, they tend to develop a grazing-dependent more than a simple grazing-tolerant strategy. These species, among which *Puccinellia maritima* is the most representative example, are capable of absorbing the chock of important biomass removal by sheep because they also propagate vegetatively or are prostrate species. As many of these species produce clones, they don't suffer from flower and fruit removal by herbivores.

A second group of species develops a grazing-tolerant strategy: species are abundant in both ungrazed and grazed areas and partly escape to herbivore uptake (i.e. they experienced a moderate reduction of height) thanks to their low stature, low palatability or high trait plasticity. This is the case of *Festuca rubra* ssp. *litoralis*, the only species that both decreases in height and increases in biovolume under grazing. For this species, the loss of height is compensated by a gain of cover maintaining a minimum biovolume.

A third group of species includes species, such as *Elymus athericus* and *Spartina townsendii* var. *anglica*, that are poorly browsed (low height reduction under grazing) and mainly distributed in ungrazed areas. These grazing-independent species probably present a low palatability compared to other species (Bärlocher & Newell, 1994; Kuijper *et al.*, 2004) and their presence is under the control of other factors such as flooding, salinity or nutrient deposit (Storey & Jones, 1978; Bakker & Berendse, 1999).

A fourth group of species gathers grazing-non-tolerant species. These species suffer from grazing pressure and hardly cope with biomass removal. Among them, *Halimione portulacoides* and *Aster tripolium* lose respectively 93% and 96% of their biovolume in grazed sites. When flocks arrive in a salt-marsh site after the withdrawal of the sea, sheep first eat *Aster tripolium* before the other plant species (personal observations). It corroborates other studies showing the severe impact of sheep grazing on the vitality of *Aster tripolium* (Kiehl *et al.*, 1996), a plant well known for its edibility (Lieth, 1999). *Salicornia* is also ranked among species highly consumed by herbivores. It is not surprising as this species is known to be a part of the sheep diet in the Somme bay, exploited for the production of the famous "Agneau de pré salé" (salt-marsh lamb). Although four main species behaviours were identified here, a gradient of intermediate strategies exists between them and is probably a response to environmental, competition and grazing gradients. This species grouping method will be proposed to shepherds as a tool to evaluate the degree of sheep pressure on plant community and to identify species sensitive to biomass removal. These results would help to modulate sheep density and to equilibrate grazing in the different parts of the bay.

CONCLUSIONS

Sheep grazing positively influences the plant species richness of the salt-marshes in Somme bay. Through cascading effects, herbivores reduce the vegetation height and biomass, control the identity of dominant species, relax competitive interaction between species for light, increase nutrient input and finally enable numerous species and various plant types to coexist in a patchy vegetation. The development of competitive tall herbs (*Halimione portulacoides* in the Somme bay but also *Phragmites australis* in the Seine estuary) is probably an outcome of landscape management and species introduction history. In most of the north-western French estuaries, successive embankments, watershed erosion, abandonment of grazing after the agricultural revolution in the 1950s and high hunting pressure limiting the natural

grazing by waterfowl have led to the spread of few dominating and tall herbs over large areas of salt-marsh (Le Neuveu, 1984). We thus greatly recommend an extensive and moderate sheep grazing to manage European salt-marshes largely dominated by highly competitive plant species. Grazed and ungrazed areas should however coexist at the landscape scale to maintain a diversified regional species pool and various habitats for the animal communities. A minimum area dominated by *Halimione portulacoides* populations should also be maintained as this species produces a major part of the salt-marsh plant biomass (Bouchard & Lefeuvre, 2000) which is used by numerous animals in local and marine trophic networks (Parlier, 2006). Some plant species heavily grazed by sheep are also used as edible and marketed agro-resources. *Salicornia*, also termed “passe-pierre”, is collected by professionals in the bay (200 000 kg/year) and cooked together with the “agneau de pré sale”; “L’oreille de cochon” (*Aster tripolium*) is also marketed as an edible delicacy; the leaves of “l’obione” (*Halimione portulacoides*) are locally and traditionally roasted as chips (as it is done with potatoes). Facing a recent increasing use of the Somme bay area by professionals, hunters, nature associations, administrations and tourists, we should quickly think how to share salt-marsh plant resources between sheep grazing and other human activities in a sustainable development perspective. In a next study, we project to monitor biomass and carbon fluxes between salt-marsh plant species and benthic animals using isotopic techniques to determine the role of grazed and ungrazed plant communities in marine food webs.

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