The effect of cattle and sheep grazing on salt-marsh vegetation at Skallingen, Denmark*

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Abstract

The aggregated effect of cattle and sheep grazing on *Puccinellion maritimae* and other salt-marsh vegetation has been studied together with changes in species composition, the percentage cover of each species, total cover and the percentage of bare ground, six years after grazing had been prevented by construction of experimental exclosures. The results of these experiments are discussed in relation to the natural development of the vegetation that occurred in a permanent plot in the ungrazed part of the salt marsh. Six years without grazing caused a marked increase in total cover and a dramatic reduction in the amount of bare ground. The species composition of the *Puccinellia maritima* community did not change during these six years, but all species increased in cover. Whereas *Artemisia maritima* migrated into the *Festuca rubra* community and only two species *Festuca* and *Halimione portulacoides,* increased in cover, all other species showed reduced cover and *Salicornia europaea* disappeared from the plot after six years without grazing. During the same period of time, three species, *Salicornia europaea, Suaeda maritima,* and *Glaux maritima,* disappeared from the plot in the ungrazed marsh as a result of natural development. During thirty-five years the vegetation originally dominated by *Puccinellia maritima* and *Salicornia europaea* has changed into a community dominated by *Halimione portulacoides,* whereas the grazed salt marsh is still dominated by *Puccinellia maritima* and *Salicornia europaea.*

These results are discussed in relation to the literature on the effect of cattle and sheep grazing on salt-marsh vegetation.

Introduction

Domestic animals have grazed on salt marshes in Denmark for hundreds of years and possibly since shortly after the transition period from a hunting culture to agriculture 2 500–3 000 BC (Mikkelsen, 1969). The written records of building dikes and intensive use of salt marshes for agricultural purposes in Denmark dates back to 1 000 AD (Warming, 1906). Grazing, hay-making, cutting grass for silage, and cutting turf for buildings are examples of the traditional agricultural uses of salt marshes and seashore meadows. Grazing by domestic animals, cattle and sheep, is so widespread and common in Denmark that only a few salt marshes and seashore meadows have been left unaffected (Mikkelsen, 1969). Consequently, grazing has affected the morphology and the vegetation of nearly all salt marshes. In order to improve the value of salt marshes for agricultural purposes, many of the marshes have been ditched and drained; and during

* Nomenclature of species follows Rostrup-Jørgensen (1973), Den danske flora, 20th ed. Gyldendal, Copenhagen.

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the last fifty years it has been common practice to fertilize the higher parts of the salt marshes. High water levels during springtime mostly determine the lower limit of areas which are fertilized, as tidal flooding may lead to severe loss of fertilizers. The traditional use of salt marshes does not include soil tilling and cultivation of crops. Although the traditional grazing of small salt marshes in Denmark has been discontinued in many areas (Vestergaard, 1978), as is the case throughout western Europe (Beeftink, 1977), open range grazing of the larger salt marshes is still economically feasible and therefore attractive.

Most of the existing information about grazing of salt marshes is based on single comparisons between grazed and ungrazed salt marshes, i.e., without experimental work (Beeftink, 1966; Schmeisky, 1974). There is very little experimental evidence for cattle and sheep grazing impeding or deflecting succession in salt marshes (Bakker & Ruyter, 1981), and even less is known about the impact of grazing on the hydrology and the salt-marsh sediments. Much of our present knowledge of how grazing animals influence artificial grassland or natural vegetation comes from agriculture where experiments with grazing have been conducted for many years (Harper, 1977). Grazing animals influence the vegetation in ways which can be generalized in six points: (1) defoliation of plants; (2) removal of plant material; (3) treading and pawing; (4) deposition of faeces; (5) deposition of urine; (6) uprooting plants, which are growing in soft sediments, during the process of grazing. The contrast between the grazed and ungrazed areas is essentially between a situation where the competitive ability is improved by the impacts of grazing and one where these impacts are disastrous.

In 1971 the Botanical Institute, University of Aarhus and the Skallingen Laboratory, University of Copenhagen, decided to initiate long-term experiments with grazing of salt marshes by domestic cattle and sheep. The aim of these experiments is firstly to gather information about the effect of grazing on salt marsh ecosystems in general and secondly to obtain specific information about the succession and vegetation dynamics in areas where traditional grazing has ceased. The present paper presents results from the first six years of experiments with *Puccinellion maritimae* vegetation.

Research area

The peninsula of Skallingen is situated on the west coast of the southern part of Jutland, Denmark (Fig. 1). It consists of an old dune system along the southwestern coast of the peninsula and a young salt marsh developed on offshore sandflats on the northeast side of the peninsula; the dune system protects the marsh from the North Sea. The salt marsh is of recent origin, having developed since the beginning of this century. See Jacobsen (1952) for details.

The sediment profile consists of a layer of fine textured sediment, consisting of approximately 60% silt, 25% clay and 5% fine sand deposited on top of coarse marine sand (Hansen, 1951). The depth of this layer varies between 5 and 20 cm and the net sedimentation rate is estimated as 0.2 cm per year (Jacobsen, 1952).

The marsh has a well-developed creek system which drains into the tidal channel Hobo Dyb (Fig. 1). The tidal amplitude is 130 cm and the salinity of the tidal water varies from 25 to 30%. There has been little or no attempt to drain the marsh. Only a few ditches have been made; none of them were cleaned since Skallingen was declared a nature reserve in 1938, and no land reclamation was

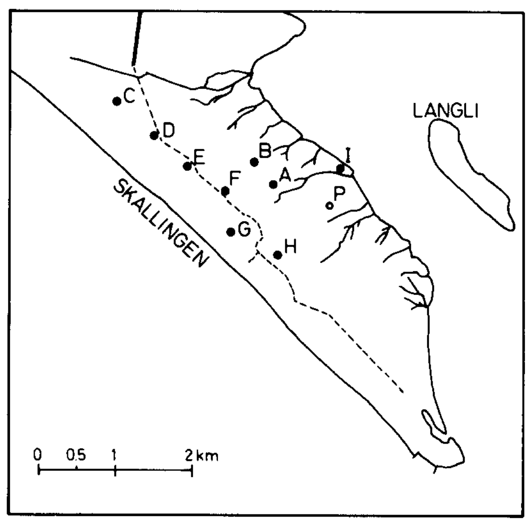

Fig. 1. Map showing the position of 8 exclosures (A-H) established during spring 1972 in Skallingen salt marsh. (P) refers to the position of the fence where the photograph shown in Figure 5 was taken. (I) shows the position of an ungrazed permanent plot established in 1969.

made. The highest tidal activity occurs during autumn and winter (Jensen *et al.*, in press). The precipitation is 750 mm per year, and the mean annual temperature is 8.4 °C (January 0.6 °C, July 16.7 °C).

Management

The Skallingen salt marsh is divided into a grazed (1 100 ha) and an ungrazed area (300 ha). The fence between the two areas runs parallel to the coast ca 400 meter inland. Ca 500 sheep and 500 head of cattle graze on the marsh from May to October; the grazing fulfills both agricultural and conservational objectives. The overall stocking level of 1/2 sheep and 1/2 head of cattle per hectare does not indicate the grazing pressure on the different plant communities. The actual grazing intensity on the preferred *Puccinellia maritima-*, *Juncus gerardii-*, and *Trifolium fragiferum*-dominated vegetation is likely to be much higher than the mean intensity. The actual grazing intensity in the various sections of the marsh is unknown.

During the last fifteen to twenty years the numbers of cattle and sheep grazing in the marsh have changed from approximately 2 500 sheep and no cattle to 500 of each, grazing the marsh in 1978 (Jensen, 1978). In former times sheep grazing was combined with hay-making (Nielsen, 1933) on some of the highest elevations in the marsh. The change from sheep to cattle grazing, the increasing number of cattle, grazing the salt marsh and the use of fertilizers will possibly result in severe changes in the salt marsh vegetation of Skallingen. The exact amount of fertilizer used in the different sections of the marsh is unknown but the farmers (pers. comm.) refer to it as a small amount.

The Skallingen salt marsh was declared a nature reserve in 1938. The preservation order of 1938 states that the peninsula is open for recreational use to the public; that hay-making and grazing of cattle and sheep are allowed; that soil tilling and construction are prohibited; and that scientists have unrestricted access for research purposes.

Material and methods

During the early spring of 1972, 8 exclosures (ca 40 m × 60 m) were established in different parts of the grazed salt marsh at Skallingen (Fig. 1) to study the effects of a sudden change to ungrazed salt marsh on the vegetation and on the sediments.

The criterion for the distribution of the exclosures within the marsh was that they should represent the different salt-marsh plant communities developed on different sediment types, water relations, soil salinities, and grazing pressure at Skallingen. In addition the exclosures should be large enough to contain homogenous stands of the plant communities.

Plant species present in each exclosure were listed and colour photographs were taken of the exclosures.

For each vegetation type, two permanent plots (1 m × 5 m) were established. One was placed within the exclosure and the other outside it. Vegetation cover was measured by the point quadrat method (Levy & Madden, 1933). A frame of ten pins made from piano wire (∅ 1.5 mm) was used for the analysis; the distance between the pins was 10 cm. 500 pins were placed systematically in each permanent plot. The results are given as mean values of percent cover. All species present in the plot were listed. The percent of bare ground was recorded from pins which did not touch plants. Species with a mean cover of less than one percent were recorded as $<1\%$.

Results and discussion

Vegetation development

The data presented in this paper were obtained from exclosures A and B (Fig. 1). These exclosures are situated in the central part of the grazed salt marsh with *Puccinellion maritimae* vegetation. It is quite productive and in high demand both from sheep and cattle, so that the grazing intensity is comparatively high. The grazed and ungrazed plots at exclosure A have a mean elevation of 5 cm above Mean High Water (MHW) which gives approximately 900 hr of inundation per year (Jensen *et al.*, in press). The mean level of the permanent plot in exclosure B is 15 cm above MHW with approximately 700 hr of inundation per year.

Figure 2 shows the result of vegetation analysis of two grazed and two ungrazed plots at exclosure A in August 1978, six years after the exclosures were

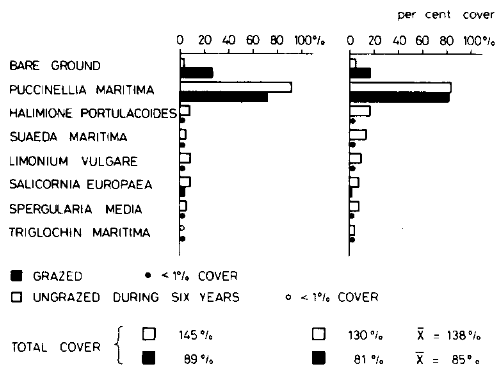

Fig. 2. Results of vegetation analyses from 4 permanent plots – two inside exclosure A and two just outside the exclosure.

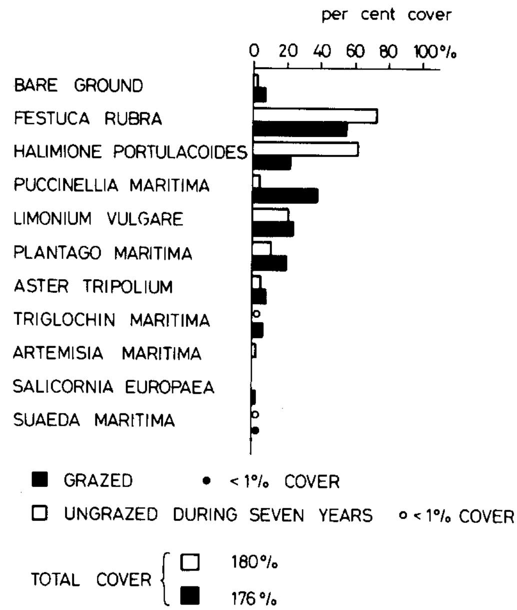

Fig. 3. Results of vegetation analyses from a permanent plot situated in the grazed part of the salt marsh. The solid bars give the species cover values of August 1971, the year before the exclosures were constructed, and the open bars give the species cover value in August 1978.

established. The total vegetation cover increased dramatically during six years without grazing; consequently the measured percentage of bare ground was reduced to a small fraction of the original percentage. No qualitative change in species composition took place during the six years, but all species increased in cover. The perennials *Halimione portulacoides* and *Limonium vulgare* showed the largest increase. The cover of the annual species *Salicornia europaea* and *Suaeda maritima* went up, although the amount of open space, i.e., bare ground, available for seedlings decreased. The quantitative change in species composition and accumulation of dead plant material changed the appearance of the ungrazed plots. The increase in number of flowering tillers and seed production was not measured but was quite evident.

Figure 3 shows the results from a permanent plot in exclosure B. The vegetation was analyzed in August 1971, the year before the exclosure was established, and in August 1978, six years after grazing ceased. In this plot the total vegetation cover was very much the same after six years without grazing, but the amount of bare ground was reduced although the percentage was less than in Figure 2.

During six years without grazing, *Artemisia maritima* migrated into the plot whereas *Salicornia europaea* disappeared from it. The percent cover of *Festuca rubra* and *Halimione portulacoides* showed a marked increase, especially *Halimione* which more than doubled in cover. This increase was accompanied by a reduction in the cover of *Puccinellia maritima* from 40% to only 5%. The cover of *Limonium vulgare, Plantago maritima. Aster tripolium* and *Triglochin maritima* was reduced to a much lesser extent.

The data shown in Figure 4 were collected from a permanent plot I, see Figure 1, situated in the ungrazed part of the salt marsh in August 1969 and in August 1978. The mean level of this plot was 17 cm above MHW and subject to inundation for ca 700 hr per year (Jensen *et al.*, in press), which means that the tidal regime of plot I was comparable to that of the plots in exclosure B. However, plot I has not been grazed by cattle and was only occasionally grazed by sheep during the late forties and early fifties, thereby serving as a reference plot to the plots in exposure A & B. Over nine years, total cover increased from 131% to 147%, mostly because of an increase in the cover of *Halimione portulacoides*, which together with *Limonium vulgare* was the only species that changed markedly in cover. Three species, *Glaux maritima, Salicornia europaea* and *Suaeda maritima* disappeared from the plot, and *Artemisia maritima* migrated into the plot during these nine years.

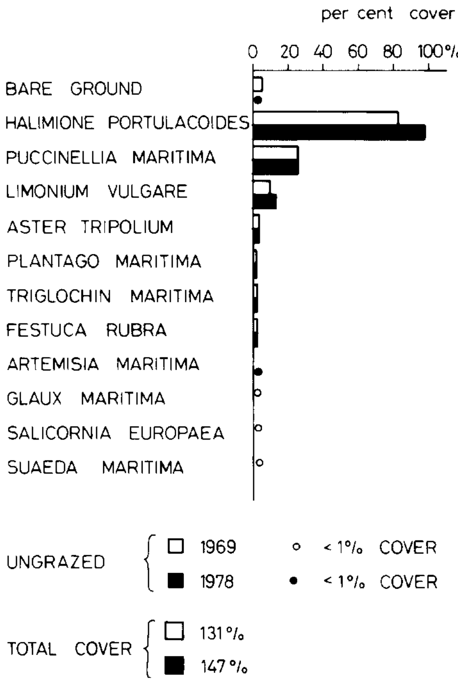

Fig. 4. Results of vegetational analyses in permanent plot (I) situated in an ungrazed salt marsh. The open bars give species cover values in August 1969. The solid bars give the species cover in August 1978. The plot remained ungrazed during the entire period.

Fig. 5. Vegetation development in a grazed and an ungrazed salt marsh. The fence is at least thirty years old. The ungrazed part has a species composition and abundance similar to results shown in Figure 4. The grazed part of the salt marsh has a species composition and abundance similar to results for grazed plots shown in Figure 2. The upper left triangle shows the grazed salt marsh.

Figure 5 illustrates the difference in appearance of the grazed upper left triangle, and the ungrazed, lower right triangle of the picture. The fences were established in the late forties, and the picture shows the constrast between a grazed and ungrazed salt marsh after ca 30 years, together with the physical damage of the vegetation by the fence because the cattle walk along the fence and thereby create a system of paths.

In 1978 the grazed salt marsh was heavily colonized by *Puccinellia maritima* with a mean cover of ca 80%. The second most important species was *Salicornia europaea* with a mean cover of ca 2–4%. Other species include *Halimione portulacoides, Suaeda maritima, Limonium vulgare, Spergularia media,* and *Triglochin maritima,* all of which had a mean cover less than 1%. The percentage of bare ground was comparatively high (22%), and the total cover in the *Puccinellia maritima* vegetation was less than 90%, which indicates that it was an open community where there is much vacant space for seedling establishment. The dramatic reduction in percentage of bare ground in the plots and the general increase in percentage of total cover after six years without grazing indicate the importance of three of the impacts mentioned earlier that grazing may have on vegetation, namely defoliation, removal of organic matter, and treading.

Grazing behaviour of cattle and sheep

Grazing animals select their food using the senses of touch, sight, and smell, and they tend to choose the more leafy portions first: young leaf > old leaf > green stem > old stem > senescent material. Sheep are very selective and may distinguish between individual leaves in a pasture (Harper, 1977); they bite leaves between the incisors of the lower jaw and a pad on the upper jaw and are therefore less hard on the root system than cattle. The sheep consistently selected forage higher in protein and lower in crude fiber (Hafez, 1975) and consumed between 1.3 and 5.0 kg of fresh herbage a day depending on age and body weight. Sheep tend to graze small patches of 16 × 16 cm and then move on to another patch (Morris, 1969) giving a mosaic of heavily and lightly grazed areas.

Cattle are far less specific and precise, partly because of the size of their jaw, partly due to their grazing procedure. Cattle walk slowly over the pasture and take successive bites by rolling their tongue round a bunch of plant material and then, with the grass held firmly between the tongue and the lower incisors, pulling or tearing it off from the sward, often with a jerking movement (Holmes, 1980). If the plants are well rooted, the leaves break off; but many plants, especially in soft sediment, may be uprooted by cattle grazing. Cattle consume between 30 and 60 kg of fresh herbage a day depending on age and body weight (Hafez, 1975). Grazing may occupy 6–11 hr per day, normally in two periods, one before dusk and one before dawn with shorter periods during the night (Holmes, 1980). Sheep spend more hours grazing than do cattle. In the salt marsh this general pattern is modified because the animals generally move to areas of high elevation as the tide comes in and then return to low areas as the tide ebbs. Cattle tend to graze vegetation in the lower moist parts of the salt marsh initially, but they move to the upper drier areas subsequently. The sheep are driven to higher elevations during the night as a part of the management (pers. comm. with the shepherd). After feeding, cattle walk to the drinking tanks and to the highest parts of the marsh to rest and ruminate, which may take 6–10 hr a day depending on the quality of the feed. The time spent on feeding and ruminating tends to increase as the quality of the feed decreases (Holmes, 1980). Cattle also tend to aggregate in the higher parts of the marsh at night; consequently their dung and urine are not evenly distributed but rather tend to be concentrated in a few areas (Hafez, 1975) which is likely to be in the upper and drier parts of the salt marsh. Tidal activity adds to the transport of faeces to higher levels. During spring tides, large amounts of dung are deposited at high levels and are conspicuous on the driftline of salt marshes. This also contributes to the transport of nutrients from the lower to the higher parts of the marsh, but even at high stocking rates the area likely to be covered with either dung or urine during one year is small. The total area receiving dung from adult cattle only covers from 0.45 m^2 to 1.5 m^2 a day distributed over 6–18 patches (Holmes, 1980; Wolton, 1979; Hafez, 1975), with proportionately smaller areas for smaller animals. For a similar weight of faeces, distribution is more widespread and uniform for smaller animals, particularly sheep because of smaller defaecations. Urine from cattle covers between 1 and 4 m^2 distributed over 6–9 patches and sheep produce 9–13 patches covering a total of 0.2 to 0.6 m^2.

The *Puccinellia maritima*-dominated areas of the salt marsh seem to be less affected by uring and dung than the higher parts of the marsh, partly because of the uneven distribution and partly because of the tides spread out the effect of dung and urine so that the background nitrogen content of the sediment is higher in the *Puccinellia* vegetation than in the areas with *Festuca rubra*. The vegetation in the higher parts of the marsh is often scorched by urine; *Festuca rubra* seems to be especially affected.

Usually pasture contaminated by dung or close to a dung patch is rejected by grazing animals for a long period, 13–18 months (Norman & Green, 1958). The urine patches are also rejected, but only for a few days after application; thereafter, cattle preferentially graze urine patches were the nitrogen content of the grass is elevated for two to three months from the time of deposition.

Frame (1976) estimated the total hoof area of a cow as 320 cm^2 and producing a pressure when standing of approximately 1.56 kg/cm^2. Sheep exert less pressure, about 0.94 kg/cm^2 over a total hoof area of 80 cm^2. The walking distance on good pasture has been estimated as 4 km/day for cows and 5 km/day for sheep. A pasture grazed by a stocking rate of 0.5 cow/ha could be completely trodden once every 160 days. A pasture grazed by 1 sheep/ha could be completely trodden 1.6 times in 160 days. The clearest demonstration of the deleterious effects of treading can be seen along fences (Fig. 5) and around drinking troughs, areas where the sward often is completely destroyed. Treading when soil moisture is high, as in salt marshes, often leads to loss of soil structure with a perched water table and development of anoxic conditions in the sediment. In the case of very soft sediment, the sward is turned into a system of hollows and hummocks. Consequently, the roots are poorly developed and can explore and extract nutrients from only a very limited volume of soil (Charles, 1979). Wind & Schothorst (1967) found that the bulk density of the surface layer of some moist soils in the Netherlands increased, due to compaction by grazing animals. Edmond (1964) found that treading by sheep reduced the production of 10 pasture species to between 9 and 77% of control. Reduction in tiller number appeared to be the main cause of the reduction in yield. From a production point of view, all treading damages pasture irrespective of soil moisture level, plant species, or kind of animal (Brown & Evans, 1973). However, hoof marks also create openings in the sward and thereby cause a finer pattern of heterogeneity which may be of importance in the population dynamics of salt marsh communities (Harper, 1977).

The impact of grazing on succession

The palatability of the different species is very difficult to determine, but *Puccinellia maritima, Triglochin maritima, Plantago maritima, Festuca rubra,* and *Aster tripolium* appear to be grazed frequently. According to the total cover and a subjective judgement of palatability and experience with the grazing in the marsh, *Puccinellia maritima* contributes a very high proportion of the feed in the lower parts of the marsh. Although the cover of *Puccinellia maritima* has increased during six years without grazing in all but one plot (Fig. 3), it contributes a smaller proportion of the vegetation cover in all plots. This is in accordance with the literature (Table 1) which indicates that *Puccinellia* is favoured by cattle and sheep, especially in the lower moister areas of the salt marsh. The markedly reduced cover of *Puccinellia* in exclosure B (Fig. 3) is probably because *Puccinellia* is a weaker competitor in this drier part of the salt marsh. Gray & Scott (1977) showed that *Puccinellia maritima* had a competitive advantage over *Festuca rubra* only under moist and waterlogged conditions. *Festuca rubra* covers 65% of the ground in this plot. *Puccinellia* may also be less competitive with *Halimione portulacoides* under drier, better drained conditions where sediment compaction due to treading may be less severe.

The soft sediment in the area of exclosure A demonstrates the impact of treading, the surface being turned into a system of hollows and hummocks which favour the vegetative propagation strategy of *Puccinellia* because grazing produces great quantities of fragments which then root readily when trodden into the moist ground. This very much resembles the situation which Ranwell (1972) named 'tread-planting' at Bridgewater Bay, Somerset. Grazing is an important factor in maintaining the almost complete dominance of *Puccinellia maritima* in those large areas of grazed salt marshes which are inundated for at least 900 hr a year by tidal flows or stagnant trapped tidal water (Jensen *et al.*, in press; Jensen, 1974).

Vegetation analyses give little information on the morphology and density of the different species. The densities of the annual species *Salicornia europaea* and *Suaeda maritima* have increased. Although the amount of open space has been reduced, the total plant cover was much higher than in grazed areas. In the first year after grazing stopped, the density of *Salicornia* in August was 12 000 individuals per m^2 (Jensen, unpubl. results), reflecting the large amount of open space available and low mortality after the grazing animals had been removed from the area. During the following years the population density of *Salicornia* was lowered because of a decrease in availability of open space. The annual species are opportunists and therefore are in a position to establish themselves very quickly whenever there is any space in a suitable area. The seed production in the area strongly influences the potential for each species to establish itself in a new area. The number of seeds produced by *Salicornia europaea* is closely related to the number of sidebranches produced, which in turn depends on the density of the stands and competition from other species (Jensen & Jefferies, in press). It was clear from the present results (Fig. 2) that the cover of *Salicornia* increased after six years without grazing, which is in agreement with the hypothesis that a high proportion of *Salicornia* seedlings are destroyed by trampling (Harper, 1977) even though most authors state the positive influence of grazing on *Salicornia,* because grazing keeps open spots suitable for germination under low competitive stress. When grazing is prevented, survival increases and seed production is higher, which in turn leads to higher population densities. After some years, however, the competition from other species

Table 1. Literature records of the impact of grazing on the salt marsh species studied in the present paper.

	Artemisia maritima	*Aster tripolium*	*Glaux maritima*	*Festuca rubra*	*Halimione portulacoides*	*Limonium vulgare*	*Plantago maritima*	*Salicornia europaea*	*Spergularia media*	*Puccinellia maritima*	*Suaeda maritima*	*Triglochin maritima*
Adriani, 1965												
Bakker, 1978, 1981	÷, LD	÷	+÷	÷, LD	÷	÷, LD	+÷	LD	+	+	LD	+
Beeftink, 1966, 1977	÷I; +÷	÷I; +÷	+÷	+÷	÷I; +÷	÷; PD	+÷	+	+	+	+÷	+÷
Boorman, 1967						÷, GR				+		
Chapman, 1950, 1960					÷	÷; PD						
Chater, 1962					÷							
Dahlbeck, 1945	÷; A	÷		÷; A		÷		+; GR;	+	+	+; GR	
Gillham, 1955				÷			+					
Gillner, 1960, 1965	÷; A	÷		×; A; GR		+÷; A	+	+; GR		+	+; GR	
Gray & Scott, 1977		÷		÷	÷	÷				+	÷	
Hintz, 1955				÷						+		
Iversen, 1936				÷								
Jensen, 1978	÷	÷	+	÷	÷	÷	+	+; GR	+	+	+; GR	+
Ketner, 1972						÷; PD		÷; PD				
Kloss & Succow, 1966						+-GR						
Kloss, 1969						+-GR						
McCrea, 1926	÷			÷		÷						
Morss, 1927						÷; PD						
Ranwell, 1961, 1968, 1972		÷			÷PD	÷;PD	÷			+		+
Schmeisky, 1974	÷			÷		÷						
Tansley, 1949				+						+		
Tyler, 1969, 1971										+		
Vestergaard, 1978		÷	+	÷		÷		+	+	+		+
Weevers, 1940						÷						
White, 1961				÷			+					
Yapp *et al.*, 1917					÷	÷						

+ = positively affected by grazing; ÷ = negatively affected by grazing; +÷ = indifferent in relation to grazing; A = avoided or neglected by cattle or sheep; GR = grazing reduces competitors; LD = local disparities; I = intensive grazing; PD = sensitive to physical damage.

will gradually reduce the population of *Salicornia* and eventually cause its exclusion from the area, as happened in exclosure B (Fig. 3) and in plot I (Fig. 4), where *Salicornia* and *Suaeda* disappeared from the plot, possibly because of competition from other species, especially *Halimione portulacoides*. The increase in cover of *Salicornia* and *Suaeda* is likely to derive from a relatively short-lived post-grazing burst in population densities. *Salicornia* and *Suaeda* may accidentally be grazed, but neither cattle nor sheep seem to graze either of these species intentionally. Ketner (1972) found a decrease in biomass in *Salicornia* in grazed areas, but there was no sign of its being grazed; hence he concluded that the decrease in production was the result of physical damage by treading. *Salicornia* and *Suaeda* are very crisp when young, but later both species develop a very fibrous central part of the stem which may make them less palatable. Both species are ion accumulators and may develop a smell or taste that cattle and sheep dislike. The positive influences of grazing on *Salicornia* and *Suaeda* appears to be indirect by reducing competitors and creating open space for seedlings.

Halimione appears to be sensitive to various sorts of physical damage (Beeftink *et al.*, 1977) and is very sensitive to human trampling; only a very limited number of passes creates a path in *Halimione* stands (Jensen, unpubl. results) which appears to be due partly to damage of the shoots and partly to compaction of the sediment. *Halimione* is sensitive to retarded aeration of the sediment (Chapman, 1950; Jensen, 1985). Consequently *Halimione* must be especially sensitive to treading by sheep and cattle, which produce a much higher pressure per cm^2. Compaction of the sediment by treading may well be an important factor in the negative effect of grazing on *Halimione portulacoides*. The present results agree with all authors listed in Table 1 and leave no doubt that *Halimione portulacoides* is suppressed by grazing. However, the present information is inconclusive about the main factor responsible for the negative effect of grazing.

The increase in cover of *Halimione portulacoides* in all plots and the increase of *Limonium vulgare* in some plots (Fig. 2), and decrease in others (Figs. 3, 4) leave a somewhat unclear picture of *Limonium* in relation to grazing. Defoliation is apparently not the major factor retarding these species since cattle and sheep seem to avoid both species, although they may be grazed accidentally by cattle. Ketner (1973) measured a decrease in production of *Limonium vulgare* in grazed areas, but since no sign of defoliation could be seen, it was concluded that the reduction was the result of physical damage.

In dense vegetation with a high total cover (Figs. 3, 4) *Limonium* seems unable to compete with *Halimione* and *Festuca*. The dramatic increase in the cover of *Halimione* (Fig. 3) caused a reduction of all other species except *Festuca*, including a reduction of *Limonium*. The ungrazed plot I showed the same reduction of *Limonium*, which could be linked to the total dominance of *Halimione*. In a vegetation with less total cover (Fig. 2), there was still space for an increase in the cover of both *Halimione* and *Limonium;* but a further increase in the cover of *Halimione* may well lead to a reduction of *Limonium*. Mechanisms that keep the vegetation cover low may have a indirect positive effect on *Limonium*. Boorman (1967) concluded that low grazing intensity resulted in enhanced growth and spread of *Limonium vulgare*, but high grazing intensities had an adverse effect on this species, which agrees with most authors (Table 1).

Sheep grazing reduced the *Festuca rubra* content of the sward (Gray & Scott, 1977). Most authors (Table 1) found that grazing had a negative effect on this species, which is in accordance with the present results where the cover of *Festuca rubra* increased after six years without grazing. The adverse effect of grazing on *Festuca rubra* may in part be due to soil compaction by treading by the grazing animals. *Festuca rubra* occurs only in the upper well-drained parts of the salt marsh (Beeftink, 1959; Jensen, 1978) and on creekbanks where the sediment is well drained, oxygenated, and under low tidal influence, with less than 700 hr of inundation. These conditions without grazing for six years resulted in the establishment of *Artemisia maritima* in the plot (Fig. 3). *Artemisia* is very sparse in the grazed part of the Skallingen salt marsh whereas it is common in the ungrazed parts of the marsh. The negative effect of grazing on *Artemisia* is possibly due to physical damage and soil compaction as there was no evidence of defoliation, which suggests that cattle and sheep avoid eating this plant and which agrees with most authors mentioned in Table 1.

Triglochin maritima seems to be grazed selectively, especially by sheep, as there was much evidence of defoliation of young leaves and bitten flowering spikes. It does not show any clear trend in relation to grazing in the present results, whereas most authors report a positive effect of grazing on this species (Table 1). The high content of readily available nitrogen in young leaves and flowering spikes of *Triglochin* (Jefferies *et al.*, 1979) may contribute to the preferential grazing of this species.

The 50% reduction in the cover of *Plantago maritima* (Fig. 3) during six years without grazing may in part be due to competition from *Halimione portulacoides*, which increased from 20% to 60% cover during the same period. A negative association between *Plantago maritima* and *Halimione portulacoides* has been shown by Boorman (1971), but there are conflicting reports in the literature on the impact of grazing on *Plantago* (Table 1).

Long-term development

Figure 5 visualizes the effect of cattle and sheep grazing on the long-term development of plant communities in salt marshes. The fence has existed for at least thirty years, and nothing but the grazing seems to differentiate the two areas. The sediment profiles are nearly identical and are typical of those of the marsh as a whole. The elevation of the two areas was almost identical resulting in equal tidal influence; but because of the different management practices in the two areas, they developed very differently. Of course, the interaction between plants and sediment also reinforces the differences between the grazed and ungrazed salt marshes. In 1933, several years before the fence was erected, the vegetation in this particular area consisted of the following species (given as the mean for three plots and rated on a scale with 10 steps, x indicating presence): *Puccinellia maritima* (10), *Salicornia europaea* (10), *Suaeda maritima* (5), *Aster tripolium* (3), *Halimione pedunculata* (1), *Spergularia media* (x), *Plantago maritima* (x) (Nielsen, 1935). In 1978 both species composition and percentage cover in the ungrazed area were similar to the vegetation in plot I (Fig. 4), and the vegetation in the grazed area was similar to the grazed plots (Fig. 2) close to exclosure A. During 45 years, the ungrazed part of the marsh developed from a community dominated by *Puccinellia maritima* and *Salicornia europaea* to a community dominated by *Halimione portulacoides* as a result on the ongoing development of this young salt marsh with sediment accumulation as the driving force. During at least thirty years of this period, grazing has retarded the succession of the vegetation in the grazed area as after 35 years it was still completely dominated by *Puccinellia maritima* and *Salicornia europaea.*

The change in the ungrazed plot I from 1969 to 1978 possibly reflects the natural succession in the salt marsh, which may not be unidirectionaly and predictable but can be impeded or deflected as a result of hydrological or climatic changes. In the future, species like *Glaux maritima, Salicornia europaea,* and *Suaeda maritima* may migrate back into the plot and the quantity of *Halimione* decrease and increase again.

Concluding remarks

For the species involved in this particular study, many observations have been reported concerning plants in relation to grazing by cattle and sheep (Table 1), and the following characteristics are associated with tolerance to such grazing: (1) plants must be able to withstand defoliation, i.e., loss of leaves, shoots and reproductive organs during the growing season; (2) root systems must be strong enough to avoid uprooting; (3) the morphology must ensure that sufficient leaf area is available for assimilation, even under heavy grazing pressure; (4) plants must have comparatively large amounts of belowground biomass and storage tissue; (5) the plant must be able to reallocate nutrients and assimilate carbon rapidly; (6) the plant must have fast regrowth after defoliation; (7) reproduction must be possible despite grazing pressure, either by seeds or formation of clones; (8) plants have to withstand treading; (9) plants must be able to tolerate deposition of dung or have a high recolonization capacity; (10) plants must tolerate being sprayed with urine.

The species composition of the plots in exclosure A was still the same six years after the change from grazed to ungrazed salt marsh, whereas three species have disappeared from the ungrazed plot I. This indicates the difficulty of predicting succession as a result of changes in the grazing regime by comparing a grazed and an ungrazed parts of the salt marsh on a single occasion. An experimental approach is necessary because the aggregate influence of cattle and sheep on the vegetation alters plant interaction and changes the interactions between plants and the environment which result in impeded succession. When grazing is terminated, a burst of post-grazing changes in the vegetation takes place, after which natural competitive and environmental interrelations are restored. The duration of this period remains to be established. Furthermore, there is an urgent need for detailed studies that resolve the combined effect of grazing on plants and the environment into its most important components: defoliation, removal and turnover of organic matter, treading, uprooting, and depositions of dung and urine.

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