Ann. Bot. Fennici 38: 181–200 ISSN 0003-455X
Helsinki 7 September 2001

How does grazing by cattle modify the vegetation of coastal grasslands along the Baltic Sea?

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Received 25 August 2000, accepted 9 October 2000

Jutila, H. 2001: How does grazing by cattle modify the vegetation of coastal grasslands along the Baltic Sea? — *Ann. Bot. Fennici* 38: 181–200.

The vegetation of four grazed and five ungrazed shore grasslands was studied in seashore and in delta on the southwestern coast of Finland. Ordinations and classifications separated delta plots from seashore plots, which were further divided into reed stand plots, epilittoral plots and geo- and hydrolittoral plots. The partitions reflected flooding stress, moisture conditions, grazing and properties of parent material. Elevation explained the data best. The primary factor in producing the vegetation zonation pattern in these Baltic coastal grasslands is the short-term fluctuation in sea-level. Although grazing was not the most important factor for explaining the variability in the data, its impact on the vegetation was considerable. *Phragmites australis* was much more common in ungrazed than in grazed plots. It dominated the hydrolittoral, was abundant in geolittoral and existed even in transition zone of the ungrazed transects. In grazed transects *Agrostis stolonifera* and *Eleocharis uniglumis* dominated the hydrolittoral. The lower geolittoral was dominated by perennial graminoids. In the middle and upper geolittoral, forbs were more frequent and abundant. In the grazed seashore transects, the lower geolittoral was dominated by *Juncus gerardii*, while in the ungrazed transects *Calamagrostis stricta*, *Agrostis stolonifera* and *Juncus gerardii* formed the zone together with *Phragmites australis*. The transition zone in the grazed transects was a narrow drift wall, in the ungrazed transects, however, it was much broader and dominated by tall growing plants. On fine-grained substrate, the epilittoral was dominated by *Agrostis capillaris*, *Carex nigra* and *Deschampsia cespitosa* and on till by *Deschampsia flexuosa* and *Galium verum*.

Key words: coastal vegetation, delta, grazing, elevation, SSH-ordination, water-level fluctuation

Introduction

Shores are constantly fluctuating border areas between water and land. The typical zonation of shore vegetation is dependent on flooding, salinity and soil properties, which change along the shore gradient. It is demonstrated in many studies (Gough *et al.* 1994, Sanchez *et al.* 1996, Grace & Jutila 1999, Jutila 1999a) that the duration and depth of flooding are the most important factors shaping shore vegetation. Shore plants, which are influenced by disturbances such as flooding, salinity, waves and ice, can try to survive the adverse conditions using avoidance strategies, such as a persistent seed bank, or tolerance strategies, such as metabolic adaptations (Crawley 1986). Most shore plants use both strategies but with varying intensities and different modes at various life stages.

Vegetation studies along the Baltic Sea have a long tradition. In Finland, the shore vegetation of the Gulf of Bothnia was studied by, e.g., Leiviskä (1908), Siira (1970), and Vartiainen (1980, 1988); that of the Gulf of Finland by, e.g., Häyrén (1902), Brenner (1921), Fagerström (1954), and Buch (1959). For the Archipelago Sea, similar work was done by, e.g., Lemberg (1933) and Palmgren (1961), and in Sweden by, e.g., Tyler (1969a, 1969b), Ericson and Wallentinus (1979), Ericson (1981), Jerling 1983, and Cramer and Hytteborn (1987). From Estonia might be mentioned the studies by Lippmaa (1934), Rebassoo (1975), and Zobel and Kont (1992). Recently Påhlsson (1994) and Toivonen and Leivo (1993) classified seashore grasslands of the Nordic Countries. However, more, modern ecological studies are needed to fulfill the needs of biodiversity conservation.

Baltic coastal meadows are natural grasslands which traditional management has enlarged to upper elevations. Until the 1940s, large areas of coastal meadows were grazed or mown, but after that management ceased and the common reed expanded heavily in many shore meadows.

During recent years the coastal areas have gained an important conservation status in Europe, which is elaborated by integrated coastal zone management. In Finland, many seashore grasslands are included in the European Natura 2000 network, and several Life-Nature projects have been carried out along the coasts of Finland. For example, in the Pori region the aim was to manage the seashore grasslands especially for the avifauna (Jutila 1997b). According to the Helsinki Commission, seashore meadows are heavily endangered biotopes along the Baltic Sea (von Nordheim & Boedeker 1998). The Finnish Nature Conservation Act, enacted in 1996, designates low-growth seashore grasslands as protected biotypes and Regional Environmental Agencies have started to map them. Still, seashores are targets of various activities, such as traffic, construction, cottage building, boating, fishing, hunting etc. For conservation planning to be effective or preferably optimal, additional information is needed on the distribution of vegetation types, of the genetic, species and biotype diversity in these communities, and the impact of different management methods.

The emphasis of this paper is placed on the composition of coastal grassland communities and the controlling environmental factors, in particular on cattle grazing. I use the data collected from three grazed and four ungrazed seashore grasslands and one grazed and one ungrazed grassland in a river delta in western Finland. The results are applicable to conservation and management of coastal grassland communities along Baltic Sea shores.

Material and methods

Study area and sites

The study area is located on the southwestern coast of Finland, by the Gulf of Bothnia, near the town of Pori (61°30´–61°33´N, 21°28´–21°41´E). Climatic variables of the area were given by Jutila (1997a), and Seinä and Peltola (1991). The Baltic Sea has practically no tides, however, seasonal and daily fluctuations in the water level are important factors influencing the shore vegetation. During the growing season the water level usually fluctuates within 20-cm limits, but changes of up to and even exceeding one meter can occur. In winter, the water level fluctuates more widely. There is a regular period of low sea level in May–June,

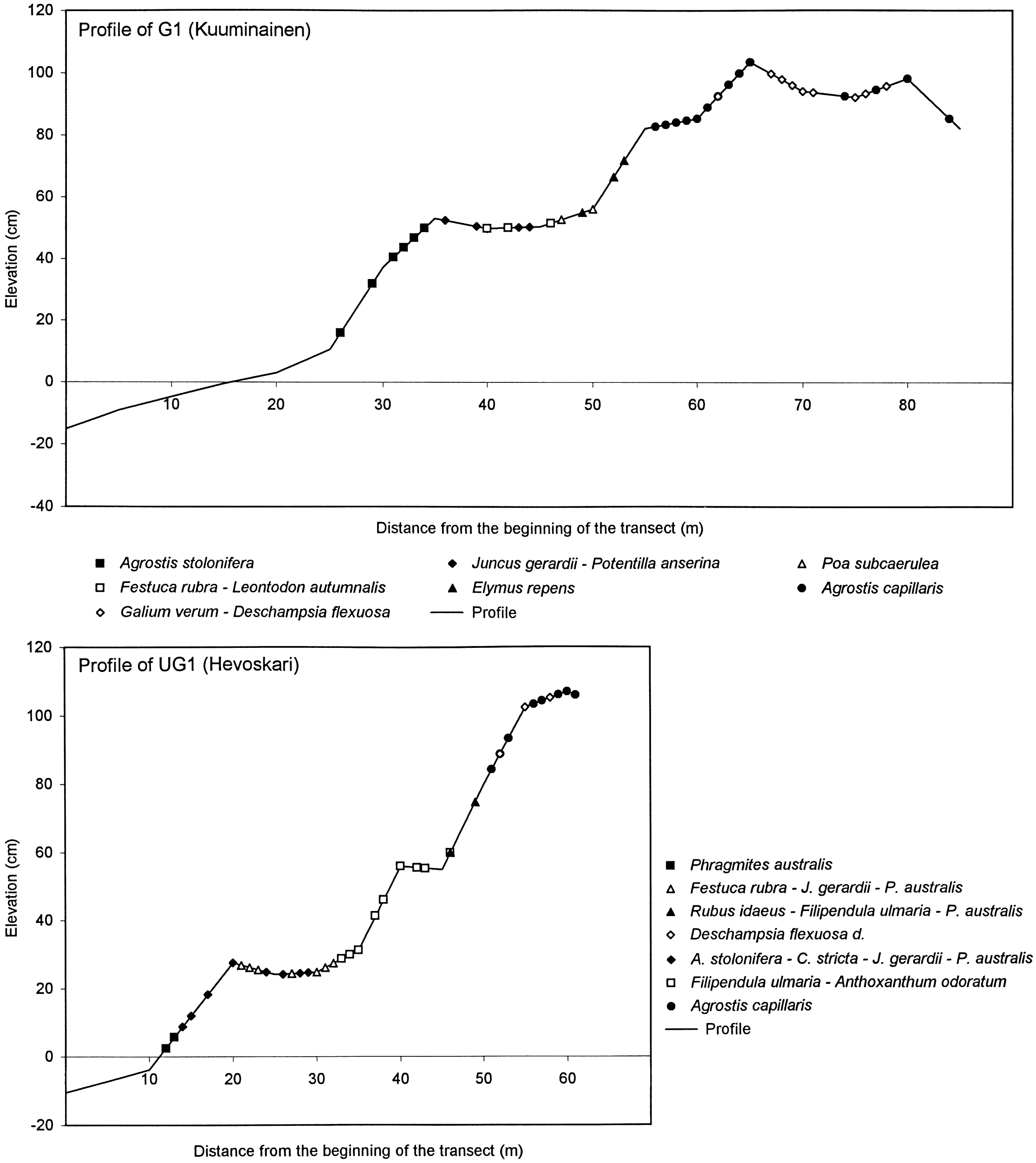

Fig. 1. Profiles and sample ordinations of transects G1 and UG1, with classification groups and their interpretation. The communities are named after the dominant species.

when the salinity of the water is also at its lowest. The land uplift rate in Pori is 7 mm per year. The study area belongs to the southern boreal zone. The bedrock is predominantly Jotnian sandstone, with occasional olivine diabase intrusions.

Four grazed and five ungrazed shore grasslands, two of them (transects G4 and UG4) in the mouth of the Kokemäenjoki and the rest at the sea, were investigated during the years 1993 and 1994 (*see* Jutila 1997a). Basic information about transects was provided by Jutila (1999b) and the profiles of the transects are shown in Figs. 1–4. The transects G1, G2 and G4 have been grazed from the beginning of this century. In the transect G3, grazing ceased in the beginning of the 1970s

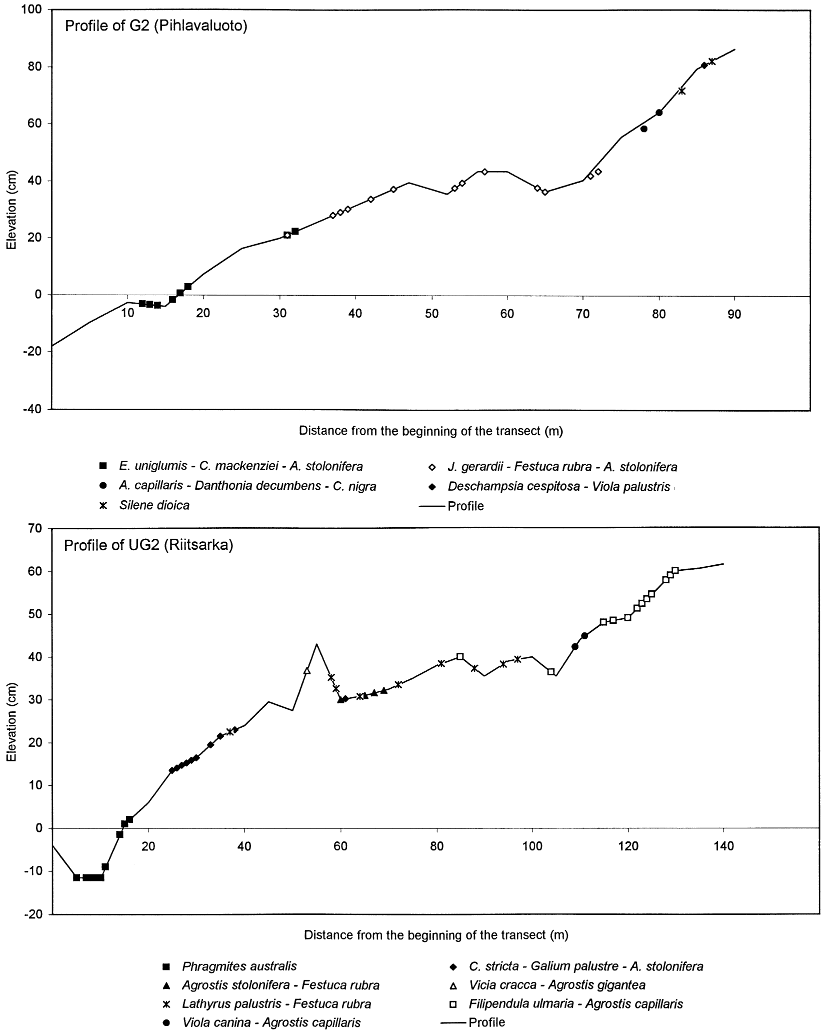

Fig. 2. Profiles and sample ordinations of transects G2 and UG2, with classification groups and their interpretation. The communities are named after the dominant species.

and was started again in 1990. The ungrazed transects have been without grazing for several decades. These grasslands are important for the avifauna, and have other conservation values as well (Jutila *et al.* 1996, Jutila 1997b).

Methods

The transects ran from waterline to the woods, through 3–5 vegetation zones, which were numbered in the same direction (*see* more in Jutila 1997a). Plant communities were described using a stratified random sampling design for each vegetation zone. A total of 411 1-m^2 plots, 201 grazed and 210 ungrazed ones, were studied in July, August and September in 1993 and in 1994 (more in Jutila 1997a). The total plant cover and the cover of each vascular plant species (%) was visually estimated in the plots. Taxonomy and nomenclature follow Hämet-Ahti *et al.* (1998) and the terminology of littoral zonation is based on Du Rietz (1930) and Gillner (1960).

In 1994, the average height of the vegetation was measured in 165 0.25-m^2 plots (within the 1-m^2 plots; 49 grazed and 116 ungrazed plots) located in most transects (not in G2 and UG3a). The total above-ground biomass (including both living and dead material) was harvested in 0.25-m^2 plots in August 1993 and 1994 (194 ungrazed

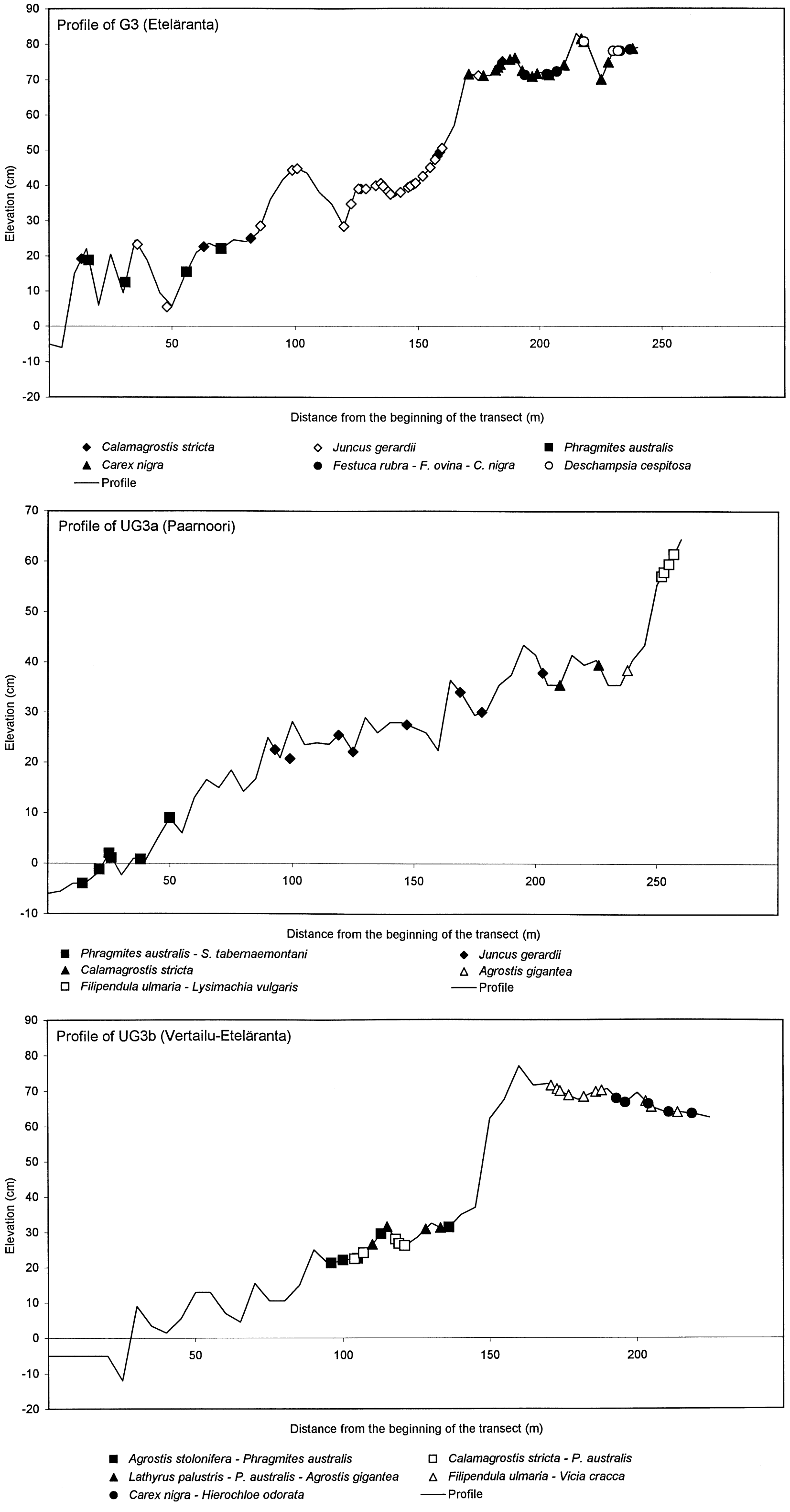

Fig. 3. Profiles and sample ordinations of transects G3, UG3a and UG3b, with classification groups and their interpretation. The communities are named after the dominant species.

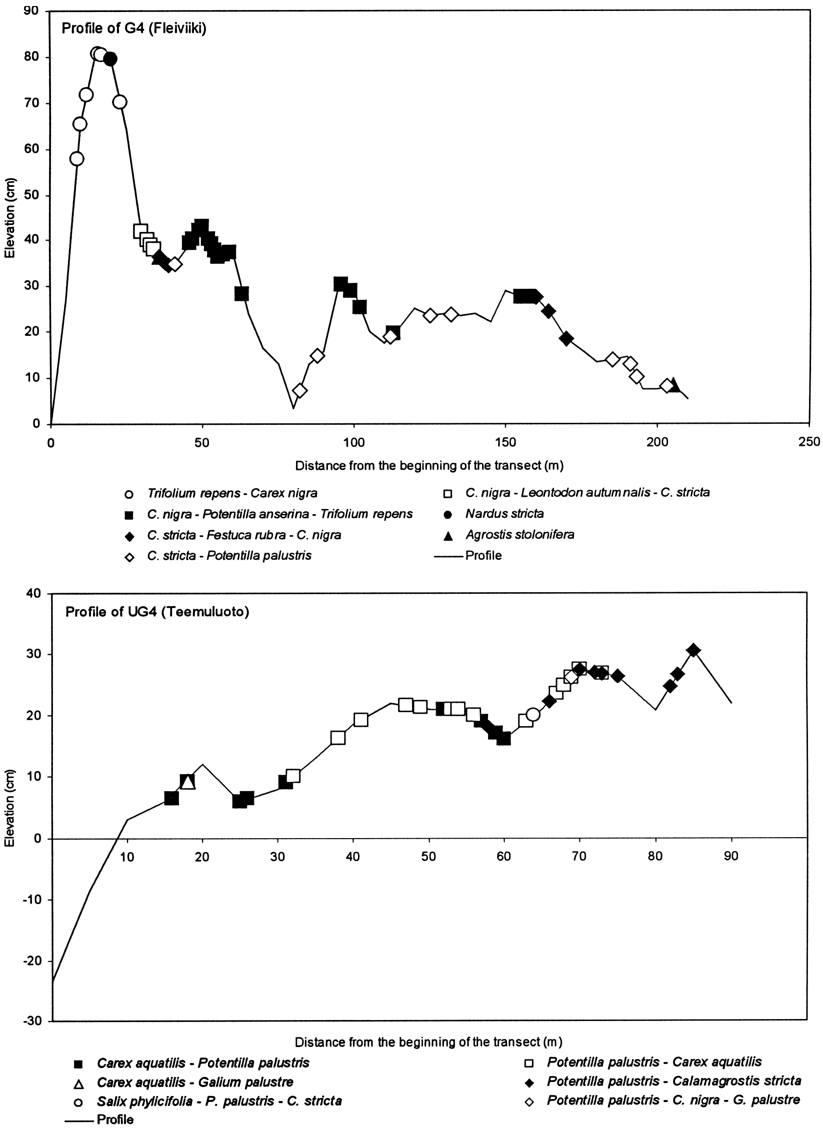

Fig. 4. Profiles and sample ordinations of transects G4 and UG4, with classification groups and their interpretation. The communities are named after the dominant species.

and 171 grazed plots). Both the dry and the fresh biomass were measured (*see* more information in Jutila 1997a). The depth of the organic layer (maximum depth, 10 cm, was reached in only four samples out of 398) was measured from the seed bank samples (gathered in the spring of 1993 and 1994). The parent material type was determined visually on the basis of seed bank samples. This method yielded six types, numbered according to diminishing grain size: gravel, sand, fine sand, silt, clay and peat. The presence of stones was recorded separately on scale 0–3 (none–many).

In 1994, the transects were levelled, with an altimeter, at horizontal intervals of 5 meters. The water level was determined according to the station data of Mäntyluoto (Marine Research Institute) and the elevation of plots was determined (*see also* Jutila 1997a). Long-term water level data (1925–1993; Marine Research Institute) was used to estimate the average time of the flooding in each sampling point during the growing season months, indicated by a stress value (Stress/5–Stress/10, corresponding to stresses from May to October) The figures are related to a theoretical mean water level.

Multivariate statistics

Multivariate statistics were run with PATN (Pattern Analysis Package; Belbin 1993). For the samples by species data I used both logarithmic, $\ln(x + 1)$, and linear transformations. The species vs. samples data were ln-transformed, and species growing in seven or fewer plots were disregarded. The similarity between the samples was counted with the ASO procedure applying the Bray & Curtis formula (*see* Belbin 1993). For species by samples data the association measure was two-step, based on the Bray & Curtis measure but taking into account the asymmetrical relationship between species. In the FUSE procedure, the samples were agglomeratively fused with flexible UPGMA, which weights objects equally in the fusion. The sample-based and species-based data were combined in TWAY, which also gives a measure, χ^2-value, for the goodness of the groupings (produced by GDEF).

As an ordination program I used SSH (Semi-Strong-Hybrid-multidimensional scaling; Belbin 1993), which uses the Guttman & Lingoes strong monotone regression and a single symmetrical matrix. This program requires selection of a dimensionality; three dimensions were mainly used. The SSH calculates an estimate, measuring the distances between input and output points. When the estimate is under 0.15, the goodness of fit is fair.

Kruskal-Wallis tests (in GSTA = Group statistics) were run to detect possible differences in the environmental parameters between sample groups. With the ordination-based PCC (multiple-linear regression program) the data scatter was fitted to the environmental parameters. This procedure gives a correlation coefficient for each environmental parameter, which can be used as a rough indicator of the importance of each attribute. Monte-Carlo randomizations (MCAO) with 100 permutations were run in conjunction with PCC module to define the significance of the correlations of the environmental variables. Multivariate statistics were run separately for different years and transects (also in combination), for seashore vs. delta data sets and for all the transects and both years taken together. The environmental variables used in statistical analyses are shown in Table 1.

Results

Flora

A total of 146 vascular plant species were found in the 411 1-m^2 plots and 183 species in the total above-ground flora of the study areas. The most abundant and the most frequent species was *Agrostis stolonifera*, occurring in 57% of the plots and having an average cover of 13.5% in these plots (7.7% in all plots). Almost as abundant was *Calamagrostis stricta* (7.5% of all plots, 17.1% of plots where it occurred). Also *Phragmites australis*, *Potentilla palustris*, *Festuca rubra* and *Carex nigra* surpassed the cover of 5% (the average covers for the plots in which these species occurred were > 10%). *Juncus gerardii* and *Filipendula ulmaria* covered 15.2% and 11.1%, respectively, of the plots in which they occurred, though the average coverage in all plots was < 5%. The maximum plot covers of all these species was ≥ 60%. The second most frequent species were *Festuca rubra* and *Galium palustre*, which were found in at least 200 plots. The other frequent species (> 100 plots) were *Carex nigra*, *Calamagrostis stricta*, *Phragmites australis*, *Potentilla anserina, Filipendula ulmaria*, *Juncus gerardii*, *Poa subcaerulea* and *Lathyrus palustris*.

About half of the species can be considered infrequent, i.e. found in ≤ 10 plots (2.4% of all the plots). There were 56 species with a sum of cover percentages < 10% (n = 411). The most interesting infrequent species found in the plots were *Atriplex longipes*, *Arabidopsis thaliana*, *Carex panicea*, *Centaurium pulchellum, C. littorale*, *Eleocharis quinqueflora*, *Elymus caninus*, and *Sagina nodosa* in the seashore and *Rumex hydrolapathum* in the delta. Five of these species were found both in grazed and in ungrazed transects, two (*Atriplex longipes* and *Arabidopsis thaliana*) only in grazed transects and two (*Carex panicea* and *Rumex hydrolapathum*) only in ungrazed transects. Of the other somewhat rare species found in the studied grasslands, but not in the plots, nine (*Cardamine hirsuta, Deschampsia bottnica, Erysimum strictum, Juncus bufonius* ssp. *ranarius, Myosotis stricta, Puccinellia distans, Rosa dumalis, Spergularia salina* and *Acorus calamus*) were found only in grazed transects, five only in ungrazed transects (*Dactylorhiza incarnata, Juncus balticus, Myrica gale, Carex disticha* and *Veronica scutellata*), and two both in grazed and ungrazed transects (*Eleocharis parvula* and *Montia fontana*).

Species distributions in respect to elevation

Elevational ranges of the most abundant and characterising species are presented in Fig. 5. *Schoenoplectus tabernaemontani* is clearly the species growing at the lowest elevation. It is actually the only truly hydrolittoral species among those presented in Fig. 5. A group of lower geolittoral species can be distinguished in the graph: *Carex mackenziei, Pedicularis palustris, Phragmites australis, Galium palustre, Calamagrostis stricta* and *Eleocharis uniglumis* in the seashore, and *Iris pseudacorus, Carex aquatilis* and *Potentilla palustris* in the delta. Typical middle geolittoral species are *Agrostis gigantea, Glaux maritima, Odontites litoralis, Plantago maritima* and *Potentilla anserina*. In upper geolittoral *Festuca rubra, Carex nigra* and *Rhinanthus serotinus* are characteristic. In the transitional zone between geo- and epilittoral, where an algal wall accumulates, *Filipendula ulmaria, Lysimachia vulgaris, Angelica sylvestris* and *Valeriana sambucifolia* dominate.

The epilittoral is divided into two zones: lower and upper. *Deschampsia cespitosa, Hierocholoe odorata* and *Agrostis capillaris* are typ-

Table 1. The variables studied, with abbreviations.

Transect (1–9)
Distance from beginning of transect (5–257 m) = Distance
Distance from transect (0–10 m)
Direction (N–E–S–W)
Elevation (–11.5 cm to 107 cm above mean sea level)
Length of transect (60-260 m) = Length
Vegetation zone (1–5) = Zone
Length of vegetation zone (10–132.5 m) = Zone length
Grazing (0–1)
Parent material type (1–6) = PMT
Stones (0–1)
Depth of organic layer (cm) = DOL
Fresh weight of biomass (13.6–763.5 g) = Fresh biomass
Dry weight of biomass (4.9–319.7 g) = Dry biomass
Stress factors during growing season = % of time point is under water (0%–100%)
Stress of May = Stress/5
Stress of June = Stress/6
Stress of July = Stress/7
Stress of August = Stress/8
Stress of September = Stress/9
Stress of October = Stress/10
Species richness per 1 m^2 = Species/m^2
Monocot species richness per 1 m^2 = Monocots/m^2
Dicot species richness per 1 m^2 = Dicots/m^2
Fern species richness per 1 m^2 = Ferns/m^2
Tree species richness per 1 m^2 = Trees/m^2
Annual species richness per 1 m^2 = Annuals/m^2
Perennial species richness per 1 m^2 = Perennials/m^2
Species richness per sum of 1 m^2 plots in transect = All species/ plots
Species richness per sum of 0.25 m^2 plots in transect
Species richness per transect (includes data from vegetation mapping; 50 m distance from transect)

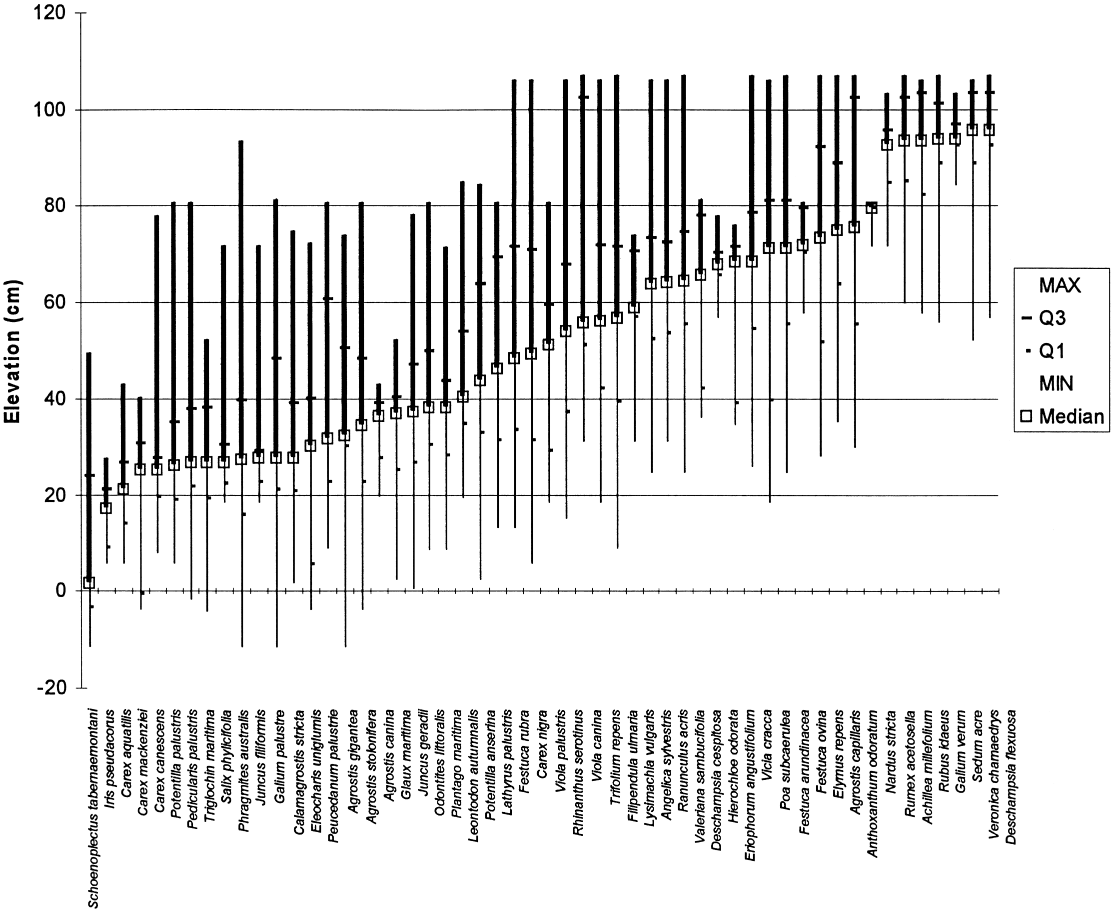

Fig. 5. Elevational ranges of 50 most common species in the seashore data. Two different colored bars for each species indicate variation from a minimum to a median and a median to a maximum.

ical species of the lower epilittoral, while *Galium verum, Deschampsia flexuosa, Sedum acre* and *Veronica chamaedrys* characterise the upper epilittoral. Based on these ranges plants were divided into hydro-, geo- and epilittoral species in the further analysis.

Plant community groups based on ordinations and classifications

Whole data

Sample classifications first separated the plots of the delta and the seashore from one another. Then the low elevation plots in the delta were distinguished from the other delta plots and ungrazed plots with dense stands of common reed were separated from the other seashore plots. Epilittoral plots differed from the geo- and hydrolittoral plots. Some partitions reflected soil properties. In species classifications the first division was between the upper and lower littoral species. Thereafter the epilittoral species were divided further and finally hydro- and geolittoral species were separated from one another.

A fairly satisfactory two-dimensional ordination of seven sample groups (Fig. 6) was obtained after log-transformation and masking the species present in seven or fewer plots (leaving 82 species). The stress in three-dimensional SSH (0.17) was quite high, but decreased clearly (0.13) when SSH was run for four dimensions. I counted the means of cover percents for each species in these seven plot groups and produced a phytosociological table

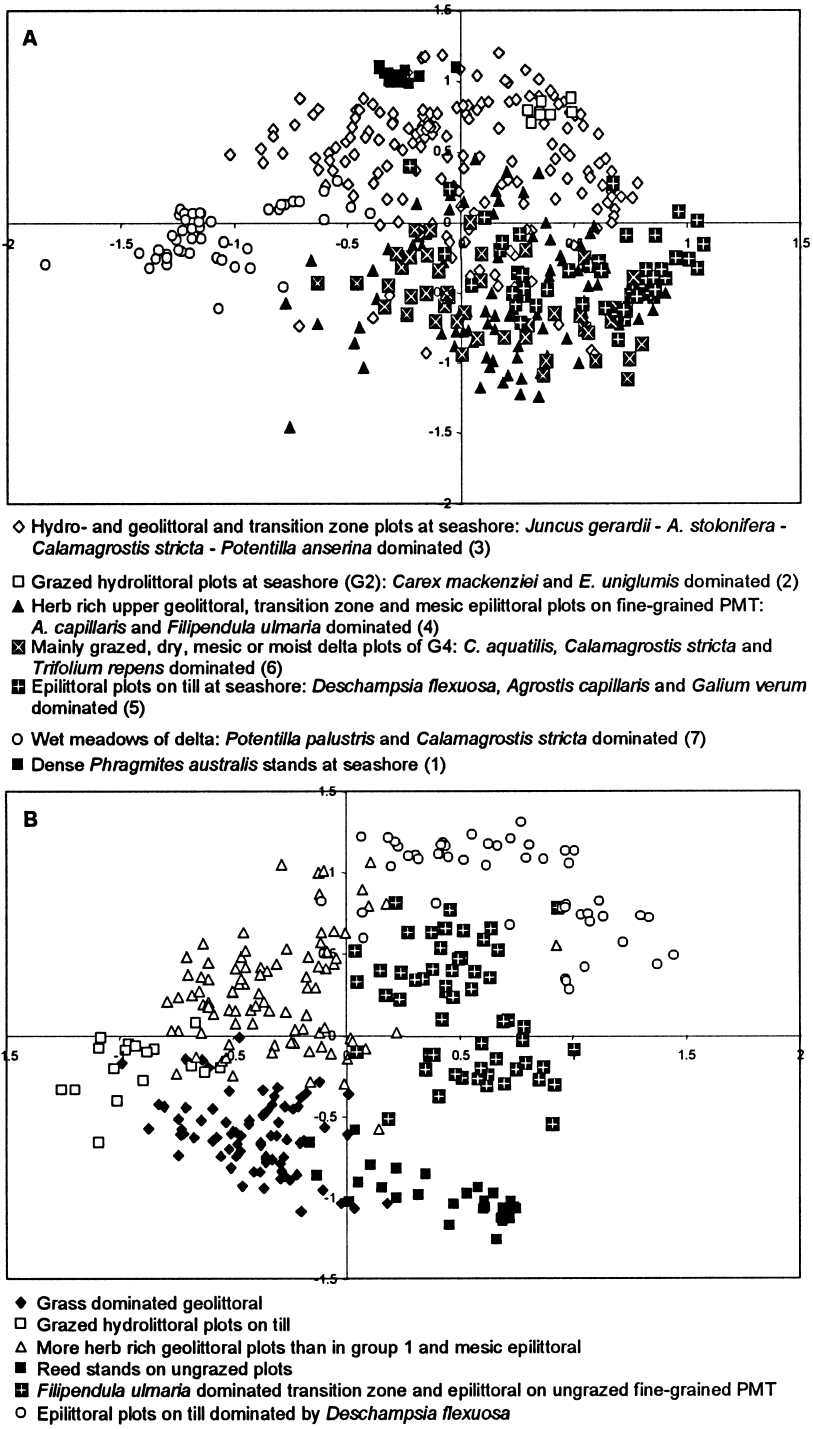

Fig. 6. Sample ordinations for (**A**) the whole data and (**B**) seashore data, with classification groups and their interpretation. The Table 2 group numbers are indicated in brackets.

where the dominants and characteristic species are presented (Table 2).

Also for the species data the stress in SSH was high, and a satisfactory ordination figure was obtained after log-transformation and masking species existing in seven or fewer plots (leaving 82 species). The species were classified by plots into nine groups.

Kruskal-Wallis non-parametric tests demonstrated significant differences in the environmen-

Table 2. Dominant and characterising species of different vegetation types, which are formed on the basis of a SHH ordination. Only 54 species are shown. Compare with Fig. 6.

	Sample groups based on SSH ordination						
Species	1	2	3	4	5	6	7
Phragmites australis	**86.00**	0.63	**8.86**	**1.46**	0.85	0.02	0.04
Triglochin maritima	**0.31**	0.13	0.97	0.00	0.00	0.00	0.00
Juncus geradii	**0.46**	0.00	**11.67**	0.48	0.00	0.00	0.00
Carex mackenziei	0.00	**28.00**	0.96	0.00	0.00	0.00	0.00
Agrostis stolonifera	0.00	**16.63**	**16.02**	**1.88**	0.13	**3.29**	**2.26**
Eleocharis uniglumis	0.00	**15.00**	1.29	0.00	0.00	0.00	0.00
Schoenoplectus tabernaemontani	0.00	**0.88**	0.35	0.00	0.00	0.00	0.00
Calamagrostis stricta	0.00	0.00	**13.10**	0.03	0.00	**9.07**	**11.15**
Potentilla anserina	0.00	0.00	**2.07**	**1.64**	0.17	**5.47**	0.00
Pedicularis palustris	0.00	0.00	**1.67**	0.00	0.00	0.00	0.00
Plantago maritima	0.00	0.00	**1.46**	0.12	0.01	0.00	0.00
Glaux maritima	0.00	0.00	**0.83**	0.01	0.00	0.00	0.00
Peucedanum palustre	0.00	0.00	**0.78**	0.10	0.00	0.01	0.14
Odontites littoralis	0.00	0.00	**0.68**	0.05	0.02	0.00	0.00
Festuca rubra	0.00	0.00	**7.73**	**7.21**	**2.61**	**6.17**	0.15
Lathyrus palustris	0.00	0.00	**4.84**	**2.30**	0.00	0.00	0.00
Carex nigra	0.00	0.00	**3.04**	**8.53**	0.62	**17.54**	0.96
Poa subcaerulea	0.00	0.00	**1.28**	**1.87**	**4.25**	**4.18**	0.15
Leontodon autumnalis	0.00	0.00	**1.10**	**0.20**	0.79	**6.22**	0.00
Agrostis gigantea	0.00	0.00	**2.00**	**0.27**	0.00	0.00	0.00
Filipendula ulmaria	0.00	0.00	0.63	**15.88**	**3.23**	0.09	0.30
Angelica sylvestris	0.00	0.00	0.27	**3.88**	0.25	0.00	0.00
Deschampsia cespitosa	0.00	0.00	0.09	**3.86**	0.00	**1.04**	0.00
Viola canina	0.00	0.00	0.00	**2.78**	0.50	0.00	0.00
Festuca arundinacea	0.00	0.00	0.09	**2.77**	**2.84**	0.00	0.00
Vicia cracca	0.00	0.00	0.20	**2.22**	**1.41**	0.00	0.00
Rhinanthus serotinus	0.00	0.00	0.41	**1.95**	0.17	0.00	0.00
Anthoxanthum odoratum	0.00	0.00	0.00	**1.92**	**2.06**	0.26	0.00
Valeriana sambucifolia	0.00	0.00	0.02	**1.69**	0.34	0.00	0.00
Lysimachia vulgaris	0.00	0.00	0.01	**1.51**	0.00	0.00	0.00
Hierochloe odorata	0.00	0.00	0.00	**1.47**	0.00	0.22	0.00
Ranunculus acris	0.00	0.00	0.02	**1.09**	0.13	0.04	0.00
Agrostis capillaris	0.00	0.00	0.04	**10.34**	**16.50**	0.57	0.00
Deschampsia flexuosa	0.00	0.00	0.00	0.08	**12.63**	0.00	0.00
Galium verum	0.00	0.00	0.00	0.02	**7.33**	0.00	0.00
Elymus repens	0.00	0.00	0.10	0.44	**3.63**	0.00	0.00
Rubus idaeus	0.00	0.00	0.00	0.22	**2.70**	0.00	0.00
Rumex acetosella	0.00	0.00	0.00	0.02	**1.45**	0.00	0.00
Veronica chamaedrys	0.00	0.00	0.00	0.01	**1.43**	0.00	0.00
Achillea millefolium	0.00	0.00	0.00	0.00	**1.20**	0.00	0.00
Sedum acre	0.00	0.00	0.00	0.00	**1.20**	0.00	0.00
Trifolium repens	0.00	0.00	0.28	2.76	0.64	**11.74**	0.00
Potentilla palustris	0.00	0.00	0.25	0.08	0.00	**2.61**	**45.53**
Festuca ovina	0.00	0.00	0.00	0.01	0.00	**2.15**	0.00
Eriophorum angustifolium	0.00	0.00	0.12	0.40	0.00	**1.68**	0.00
Juncus filiformis	0.00	0.00	0.18	0.00	0.00	**1.20**	0.02
Viola palustris	0.00	0.00	0.01	0.91	0.00	**1.02**	0.00
Carex aquatilis	0.00	0.00	0.00	0.00	0.00	**0.76**	**17.47**
Agrostis canina	0.00	0.00	0.00	0.00	0.00	**0.75**	0.13
Nardus stricta	0.00	0.00	0.00	0.93	0.00	**0.35**	0.00
Salix phylicifolia	0.00	0.00	0.18	0.01	0.00	**0.24**	**1.87**
Carex canescens	0.00	0.00	0.18	0.03	0.00	0.09	**2.85**
Galium palustre	0.08	0.00	2.72	0.47	0.02	0.48	**7.36**
Iris pseudacorus	0.00	0.00	0.00	0.00	0.00	0.00	**1.23**

tal parameters between the aforementioned classification groups. Elevation explained the plot scatter best in sample ordination (correlation 0.85; Table 3). Also grazing and vegetation zone showed a fair correlation (0.72 and 0.71, respectively) with the data. Some groups could be separated by the parent material (correlation with the data scatter 0.61) and some by biomass (i.e. reed stands). The total vascular plant species richness in all transect plots (1 m^2) correlated fairly closely with the vegetation data scatter (0.71). The correlation coefficients of the principal axis correlations (PCC) are shown in Table 3.

Delta

The delta data (n = 91) were first divided by numerical classification according to elevation and moisture (Fig. 6). The wet group included some grazed plots (*Potentilla palustris–Carex aquatilis* dominated) and all ungrazed plots, which were further divided into *Schoenoplectus lacustris–Eleocharis palustris* plots at the lowermost elevation, then *Potentilla palustris–Carex aquatilis* plots, moist *Calamagrostis stricta–Carex aquatilis–Potentilla palustris* plots, and at high elevation plots dominated by *Salix phylicifolia*. Most of the grazed plots were at a somewhat higher elevation and were further divided into a dry *Nardus stricta* grassland plot, dryish *Trifolium repens–Festuca ovina–Carex nigra* dominated plots, mesic *Carex nigra–Potentilla anserina–Trifolium repens* plots, and moist *Calamagrostis stricta–Festuca rubra–Potentilla palustris–Carex nigra* dominated plots (Fig. 4). The ordination scatter of the five sample groups (not shown) was fairly clear and the stress in three-dimensional SSH was fair (0.12).

Table 3. Correlation coefficients of principal axis correlation for the whole data, seashore data and delta data. For the whole data the result of MCAO, the test of significance is given at the 0.01 level for the PCC value.

Variable	Whole	*P*	Sea	*P*	Delta	*P*
Distance	0.32	0.01	0.57	0.01	0.60	0.01
Elevation	0.85	0.01	0.87	0.01	0.80	0.01
Length	0.23	0.01	0.46	0.01	0.84	0.01
Zone	0.71	0.01	0.79	0.01	0.35	0.01
Zone length	0.48	0.01	0.53	0.01	0.63	0.01
Grazing	0.72	0.01	0.70	0.01	0.84	0.01
PMT	0.61	0.01	0.37	0.01	0.72	0.01
Stones	0.16	0.01	0.21	0.01	–	
DOL	0.27	0.01	0.34	0.01	0.59	0.01
Fresh biomass	0.58	0.01	0.56	0.01	0.78	0.01
Dry biomass	0.57	0.01	0.55	0.01	0.78	0.01
Stress/5	0.54	0.01	0.56	0.01	0.47	0.01
Stress/6	0.56	0.01	0.58	0.01	0.56	0.01
Stress/7	0.60	0.01	0.62	0.01	0.59	0.01
Stress/8	0.61	0.01	0.64	0.01	0.63	0.01
Stress/9	0.66	0.01	0.69	0.01	0.71	0.01
Stress/10	0.70	0.01	0.73	0.01	0.75	0.01
Species/m^2	0.53	0.01	0.62	0.01	0.32	0.01
Monocots/m^2	0.34	0.01	0.44	0.01	0.49	0.01
Dicots/m^2	0.64	0.01	0.70	0.01	0.26	0.01
Annuals/m^2	0.17	ns.	0.21	0.01	0.35	ns.
Perennials/m^2	0.55	0.01	0.63	0.01	0.30	0.01
All species/plots	0.71	0.01	0.24	0.01	0.59	0.01

– = no variation

Kruskal-Wallis non-parametric tests revealed significant differences in environmental parameters between the five groupings. Elevation, which is related to the flooding influence, showed a fair correlation (0.80, *see* Table 3) with the plot scatter in ordination. Dry grasslands were at highest (65–80 cm) level. Wet grasslands, which were at lowest level (20 cm), had thickest organic layer, highest dry and fresh weight, and finer parent material type than dry grasslands. The correlation coefficients of the principal axis correlations (PCC) are shown in Table 3 and by transects in Table 4.

Seashore

When only seashore data (n = 320) were used, the first divisions separated ungrazed plots dominated by common reed and the next divisions were between upper and lower littoral samples. Further, the upper littoral data were divided into two groups: dry, epilittoral plots on till and finer-grained, moister plots in the transition zone of geo- and epilittoral (Fig. 6b).

In the hydrolittoral of ungrazed transects, there was typically a reed belt (*Phragmites australis* belt in Vartiainen 1980) that was at its most vigorous in UG2 (height over 2 meters). In UG1 the height of the narrow common reed belt was lower (about 1.5 m) and there were numerous accompanying species. In G1 and G2, where grazing had continued for decades, the reed stands had vanished, and *Agrostis stolonifera* (in G1), *Carex mackenziei* and *Eleocharis uniglumis* (in G2; *Carex mackenziei* grasslands in Vartiainen 1980) dominated the hydrolittoral.

The geolittoral was divided into three vegetation zone groups, differing in elevation. The lower geolittoral was dominated by perennial graminoids, such as *Agrostis stolonifera*, *Juncus gerardii*, *Calamagrostis stricta*, *Phragmites australis* and *Carex mackenziei*. *Pedicularis palustris* and *Triglochin maritima* were also typical. In the middle geolittoral there were some forbs, like *Potentilla anserina* and *Lathyrus palustris*, along with the graminoids, while in the upper geolittoral more forbs accompanied dominant grass, *Festuca rubra*.

In the ungrazed transects the transition zone was indicated by tall plants, such as *Filipendula ulmaria*, *Anthoxanthum odoratum*, *Agrostis gigantea*, *Vicia cracca*, *Angelica sylvestris*, *Phragmites australis* and *Valeriana sambucifolia*. In the grazed transects mainly the same species were dominants, but the vegetation height in the drift wall was much lower.

The epilittoral vegetation was divided into two groups, which differ in elevation and parent material type and thus also in species composition. The ungrazed plots on the fine-grained lower epilittoral had mesic *Alnus glutinosa* forest with *Filipendula ulmaria* and *Lysimachia vulgaris* (plots in end of the transect UG3$_a$) or *Hierochloe odorata* grassland (plots in UG3$_b$). The grazed plots in the lower epilittoral were generally dominated by *Agrostis capillaris*, *Carex nigra*, *Festuca rubra*, *Deschampsia cespitosa*, and *Poa subcaerulea*. The plots on a coarser-grained substrate (till) at higher epilittoral had only few but highly characteristic species, such as *Deschampsia flexuosa* and *Galium verum*.

The seashore data set was very heterogeneous and overlapping and the ordination presented in Fig. 6. was obtained after transforming data to a linear scale and masking subordinate species (if a sum was less than 15; only 40 species were left). The ordination groups for each transect are presented on transect profiles in Figs. 1–3 and the correlation coefficients by transects (PCC) in Table 4.

Kruskal-Wallis non-parametric tests revealed significant differences in environmental parame-

Table 4. Correlation coefficients of principal axis correlation for separate transects

Variable	G1	UG1	G2	UG2	G3	UG3$_a$	UG3$_b$	G4	UG4
Distance	0.95	0.96	0.95	0.97	0.88	0.93	0.91	0.77	0.76
Elevation	0.95	0.95	0.91	0.98	0.92	0.96	0.96	0.87	0.76
Zone	0.91	0.92	0.93	0.89	0.90	0.95	0.96	0.81	0.55
Zone length	–	0.85	0.74	0.86	0.82	0.90	0.96	0.66	0.55
PMT	0.47	0.24	0.65	0.33	0.14	0.29	0.89	0.58	0.47
Stones	0.09	0.29	0.51	0.21	–	–	0.32	–	–
DOL	0.68	0.41	0.52	0.62	0.36	0.41	0.21	0.63	0.39
Fresh biomass	0.84	0.57	0.71	0.72	0.61	0.50	0.83	0.84	0.53
Dry biomass	0.72	0.57	0.53	0.72	0.64	0.44	0.84	0.81	0.69
Stress/5	0.29	0.61	0.79	0.89	0.40	0.88	0.77	0.74	0.73
Stress/6	0.33	0.65	0.80	0.91	0.50	0.87	0.80	0.78	0.74
Stress/7	0.33	0.69	0.83	0.95	0.54	0.89	0.86	0.80	0.75
Stress/8	0.32	0.71	0.83	0.96	0.60	0.90	0.82	0.82	0.76
Stress/9	0.41	0.79	0.85	0.97	0.67	0.91	0.88	0.85	0.77
Stress/10	0.54	0.83	0.86	0.97	0.72	0.92	0.91	0.86	0.77
Species/m^2	0.45	0.55	0.95	0.88	0.55	0.84	0.84	0.29	0.77
Monocots/m^2	0.42	0.44	0.49	0.76	0.49	0.87	0.72	0.22	0.63
Dicots/m^2	0.56	0.67	0.95	0.88	0.56	0.90	0.80	0.34	0.66
Annuals/m^2	0.36	0.17	0.65	0.63	0.25	0.41	0.57	0.54	0.62
Perennials/m^2	0.56	0.61	0.94	0.86	0.59	0.84	0.82	0.24	0.77

– = no variation

ters between the six groups. They differed most clearly by elevation, which showed the highest correlation (0.87, *see* Table 3) with the plot scatter in ordination. Vegetation zone and stress values for the end of growing season also showed a good correlation with the data (Table 3). In some transects also the distance from the water line showed a fairly high correlation with the data scatter, but when the whole seashore data set was used the correlation declined. The correlation between grazing and the sample scatter was 0.70.

The epilittoral group 6 had the most coarse-grained soil type with many stones (till). The organic layer was thickest in some geolittoral plots (groups 2 and 4), but thinnest in reed stands (in group 1). Dry and fresh biomasses were the highest in reed stands and the lowest in the epilittoral (group 6).

The species richness and especially the dicot richness were both correlated with the sample ordinations (61% and 69%, respectively; Table 3). Ungrazed reed stands had the lowest species richness, while plots in the epilittoral and on fine-grained substrate (group 5) had the highest species richness. Upper geolittoral plots (group 4) and epilittoral plots on till (group 6) also had a fairly large number of species. Exposed hydro- and geolittoral on till (group 2) were species poor. Hydro- and geolittoral plots (groups 1 and 3) had no trees or pteridophytes. Upper geolittoral and mesic epilittoral (groups 4 and 5) contained more annuals than the other groups. The correlation coefficients of the PCC are shown in Table 3.

Grazed and ungrazed plots

The ordination scatter of grazed and ungrazed plots covered mainly the same area except that the outermost plots enlarged the scatter to one direction in the case of grazed plots and to another in the ungrazed plots. The second axis of the ordination can be interpreted as a grazing effect. Grazed hydrolittoral plots dominated by *Eleocharis uniglumis* and *Carex mackenziei* formed an own group in the ordination, and so did ungrazed, dense reed stands plots. A classification to 12 sample groups yielded five groups with only grazed data and three groups with only ungrazed data.

Discussion

The vegetation of the coastal grasslands showed out to be diverse (in total 183 species in above-ground vegetation and in total 205 species if the seed bank is included, Jutila 1998a). The vegetation is clearly divided into zones, which differ mainly in the abundances of species but also in the species composition. Only the most frequent species were found in more than half of the plots.

Delta

In the delta, flooding is less frequent, stressful (due to fresh water) and predictable than in the seashore. Riverine sediments are in the delta fine-grained and nutrient-rich. Therefore, the vegetation of the delta and of the seashore differ in species composition and abundance as the results indicate. In the delta hydrolittoral, there is *Schoenoplectus lacustris*, while in seashore it is replaced by *S. tabernaemontani*. In the delta geolittoral, *Carex aquatilis* and *Potentilla palustris* dominate while, in the seashore, the corresponding species are *Juncus gerardii* or *Calamagrostis stricta* and *Potentilla anserina*, respectively. In the delta, the conditions for plants to grow are better (in general lower stress values and more resources) than in the seashore, leading to quick growth and greater competition for light. Most plant species in the delta grassland can be regarded as competitive tolerance strategists, but mud flat annuals are examples of avoidance strategists, which occur in the seed bank until conditions are suitable for them, such as during draw-down.

The vegetation types in the delta reflected elevation and were related to moisture conditions and grazing effect. Jean and Bouchard (1993) reported that plant community composition was correlated with the water level and the thickness of organic layer. Although the ungrazed transect was at a lower elevation than the grazed one, causing largely the differences in the vegetation, certainly, grazing was also responsible of some differences. In ungrazed grassland *Carex aquatilis* was clearly the dominant grass in the lower littoral. In the grazed transect it grew together with *C. nigra*, and was confined to somewhat wetter places than *C. nigra*.

In the grazed delta grassland (G4), grazing had kept the willow shrubs away and even conserved halophyte relict species, such as *Juncus gerardii* (not found in the study plots). Grazing which has proved to be beneficial management method for many meadow species (when applied properly), also increases vegetation diversity on the landscape scale based on the total species numbers in a larger area.

Seashore

The vegetation types found on the seashore bear considerable resemblance to the types reported by Tyler (1969a, 1969b) and Vartiainen (1980). The vegetation types in grazed and in ungrazed seashore grasslands were condensed to Table 5, mainly based on the results of this study, but some other data from the same seashore grasslands have also been used to compile it.

The hydrolittoral was dominated by reeds (*Phragmites australis* and *Schoenoplectus tabernaemontani*) in ungrazed transects and by those or other helophytes (e.g. *Eleocharis uniglumis*) or bare soil in grazed transects. Similar vegetation types dominated the hydrolittoral also in the study of Vartiainen (1980). Bakker *et al.* (1997) reported an increase of *Phragmites australis* after cessation of grazing in brackish marshes and estuaries of the Wadden Sea. It is a well-known fact that when grazing and mowing ceased along the Baltic Sea shores, many of the flat meadows were invaded by common reed (*Phragmites australis*) or, in upper parts, by

Table 5. Dominant plant species in different elevation zones of grazed and in ungrazed seashore meadows.

	Grazed	Ungrazed
Hydrolittoral		
	Eleocharis acicularis	*Phragmites australis*
	Schoenoplectus tabernaemontani	*P. australis–S. tabernaemontani*
	A. stolonifera–Eleocharis uniglumis	*A. stolonifera–P. australis*
		Agrostis stolonifera–Calamagrostis stricta–Juncus gerardii–Phragmites australis
Geolittoral		
	Juncus gerardii	*Juncus gerardii*
	Poa subcaerulea	
	Festuca rubra–Leontodon autumnalis	*F. rubra–J. gerardii–P. australis*
	Calamagrostis stricta	*Calamagrostis stricta*
		C. stricta–P. australis
		Lathyrus palustris–Festuca rubra
		L. palustris–P. australis–A. gigantea
Transition zone		
	Elymus repens	
	Agrostis gigantea–Angelica sylvestris	*Agrostis gigantea (–Vicia cracca)*
		Filipendula ulmaria–Anthoxanthum odoratum–P. australis–A. capillaris
Epilittoral		
	Agrostis capillaris	*Agrostis capillaris (–Viola canina)*
	Galium verum–Deschampsia flexuosa	*Deschampsia flexuosa*
	A. capillaris–Danthonia decumbens –Carex nigra	
	C. nigra–A. capillaris	*Carex nigra–Hierochloe odorata*
	Festuca rubra–F. ovina–Carex nigra	
	Deschampsia cespitosa–Viola palustris	
	Deschampsia cespitosa	
	Silene dioica	
		Filipendula ulmaria–Vicia cracca
		F. ulmaria–Lysimachia vulgaris

trees. This happened even to such an extent that seashore meadows with short vegetation are protected in the new Finnish law for nature conservation. *Phragmites australis* is a very competitive species, which effectively uses resources and as a tall plant shades other species: It has in many places produced large monotypic stands. In G3, the hydrolittoral reed stand continued to the geolittoral because the lowest parts of the grazed transect were actually fenced out of the pasture and so they were ungrazed. Furthermore, the duration of recent grazing in G3 is short (since 1990) and has occurred mainly at the end of the season.

Agrostis stolonifera, Calamagrostis stricta and *Phragmites australis*, which grow rapidly and are found in the lower littoral, have an advantage in the primary succession (Vartiainen 1980). In the grazed seashore, the lower geolittoral was dominated by *Juncus gerardii*, while in the ungrazed transects *Calamagrostis stricta*, *Agrostis stolonifera* and *Juncus gerardii* (similar types in Vartiainen 1980) formed the zone together with *Phragmites australis*. The latter was a highly visible and fairly important accompanying species, although its height and biomass were much lower than in the hydrolittoral.

The transitional zones between the geo- and epilittoral differed clearly between grazed and ungrazed areas. In the grazed transects, this zone was a narrow drift wall with algae or reed shoots etc., while in ungrazed transects it was much broader, indicated by tall, quickly growing plants and the drift material was less visible (also reported by Ericson & Wallentinus 1979 and Tyler 1969b). Furthermore, the vegetation boundaries in general seem to be more distinct in grazed than in ungrazed grasslands, which was also noticed by Bakker and Ruyter (1981). Taller geolittoral vegetation in the ungrazed grasslands collects litter and sediment at lower positions than shorter vegetation in the grazed ones. According to Grumblat (1987) and Andresen *et al.* (1990) the sedimentation rate is higher in ungrazed than in heavily grazed sites in the *Puccinellia maritima* zone and the transition to the *Festuca rubra* zone

Even at a fixed elevation there are various species communities due to local variations in water salinity and in the physical and chemical composition of the soil (Siira 1970). According to Ericson (1977), the sub- and hydrolittoral vegetation is largely influenced by salinity, while in the geolittoral ground- and soil-water drainage are more important factors. According to Siira (1985) saline soils are formed in the geo- and epilittoral, under dry early summer conditions, and grazing favors the formation of salt patches (Siira 1970). There were some saline patches in the pasture neighbouring G3, but they did not occur in the transects.

A wave-washed, boulder substrate seems to have long-lasting importance for vegetation (Ericson 1981). In the ordinations and classifications of my data, the boulder shores formed a separate group both in the geolittoral and in the epilittoral.

In the seashore, many species combine tolerance and avoidance strategies: they are perennial and tolerant and have a seed bank and well-dispersed seeds. In the geolittoral, plants have to tolerate flooding and salinity and in the epilittoral drought in grasslands or shade in wooded areas. Submersion under seawater leads to poor aeration and oxygen deficiency (Siira 1970).

The variable showing the best correlation with vegetation was elevation (similarly to Siira 1970, Cramer & Hytteborn 1987, Autti 1993). This indicator variable actually integrates a number of separate variables, including flooding, land uplift, salinity and ground water effect. Short-term fluctuation in sea-level is the primary factor in producing the vegetation zonation pattern of the Baltic seashores (reported also by Ericson 1980, Jutila 1997a, Grace & Jutila 1998), and the fluctuation is probably one of the primary factors in other shores as well (Grace & Pugesek 1997, Pollock *et al.* 1998).

The extreme water levels are critical factors in the generative or vegetative establishment of species. It has been expected that most of the germination in the Baltic seashores occurs in the spring when the seawater is at a low level and the meadows are influenced by freshwater. Thus, seedlings avoid flooding and salinity stress. In addition, there is free space for germination because winter and fall storms have cleaned the shores of dead and loose plant material. The environment is suitable for germination if cold and dry conditions do not inhibit it. However, the germination of some species occurs also at the end of growing season (Jutila 1998b). The fall germination is confined to higher elevations due to higher sea water levels. Indeed limitations caused by flooding at the end of growing season explained the vegetation scatter well in this study. Ericson (1980), who reported that water level correlated poorly with the vegetation, used annual water level data, which show considerable changes from one year to another, while I used long-term inundation data, covering a period of 68 years.

At seashores, there is a small and significant downward migration trend in the vegetation due to the land uplift (approximately 7 mm/year in the study area). The effects of land uplift can be observed only over periods longer than ten years; over shorter time scales, the year-to-year variation is more important (Cramer & Hytteborn 1987). It has been suggested that the land uplift offers competition free sites for plants. Ericson (1980) observed that the colonization rate at the lower shore is much higher than in the epilittoral, where the vegetation cover is already closed. Flooding and wave action can also create competition free gaps. However, Keddy (1984) has suggested that on the lakeshores of Nova Scotia there is no general release from between-species competition even on the most exposed shores. I assume that competition occurs also in the lower parts of the shore, in reed stands with a high biomass, but only rarely on the bare waterline, which suffers from disturbances and can only be colonised by a small pool of species. Vegetation cover closes more quickly in fine-grained sheltered shores than in coarse-grained exposed shores, due to less wave action, more soil to establish and more seeds in the fine-grained soil, which also retains moisture better. Earlier exposed and recently more sheltered shores along bays in the outer or middle archipelago have usually the most diverse flora, because there is some release from the harshest disturbances, but vegetation cover has not yet closed and competition is less intensive. In the most exposed shores the vegetation zones are poorly developed. They are often coarse-grained and the profile is steep.

Exposure, salinity and substrate influence the selection among species diaspores. These factors are interconnected and the subdivision of shores into a freshwater zone (in delta G4 and UG4), an inner skerry zone (seashore transects) and an outer skerry zone (Ericson 1981) includes changes in salinity (increasing towards the sea), exposure (increasing towards the sea) and matrix (coarsening towards the sea). In this study the order of exposure from the most to the least exposed transect, is G1, UG1, G2, G3, UG3$_b$, UG3$_a$, UG2. G1 is most clearly distinct from the others.

The effects of grazing on the vegetation have been dealt with in depth by Jutila (1999a). As the ordinations show, the grazing influence is not so strong as the effect of elevation. According to Bakker (1985) grazing causes retrogressive succession, of which there were signs also in this study.

Grazing and management of coastal meadows

The fact that more somewhat rare species were found in the grazed grasslands (in the total flora) than in the ungrazed ones, gives some support to the observation of Gibson *et al.* (1987) that grazing favours rarer species. There were 156 species in the grazed transects and 143 in ungrazed ones. When 116 of the species were common to both grazed and ungrazed areas, this makes 40 species only found in grazed areas and 27 only in ungrazed ones. If we look at the total flora of the traditional rural pastures, where the grazed transects were located, more rare species can be found: *Hippuris tetraphylla* (vulnerable species), *Bolboschoenus maritimus*, *Draba incana, Puccinellia distans* ssp. *borealis, Chara braunii* (a green alga), and *Ganoderma lucidum* (a mushroom).

However, as elaborated in Jutila (1994, 1997a) and Grace and Jutila (1998) the species richness of seashore grasslands was higher in the ungrazed than in grazed areas; this was evident both in the α, β and γ diversities based on the plot, and the transect data. The cumulative species richness curve (Jutila 1997a) for the ungrazed plots increased more quickly than the one for the grazed plots, but in the epilittoral the both had attained approximately the same level. Grazing seemed to decrease the species richness in the hydro- and geolittoral, but there were some indications of the positive effects of grazing in the epilittoral. Apparently, the scale of the study has important effects on the results of the grazing influence. This is related to the fact that grazing seems to produce a coarse-grained pattern in vegetation.

Grazing decreased the total cover of vascular plants in these grasslands (Jutila 1999a). Grazing increased the abundance of some species and decreased that of others. Monocots more often benefited from grazing than suffered from it (Jutila 1999a). The water level fluctuation stress and salinity probably make seashore meadows, which are in the beginning of primary succession, more sensitive to grazing than some other ecosystems. The already narrow species pool is narrowed further by grazing. According to Tyler (1969b) most seashore species are negatively affected by grazing, although the most frequent species seem rather indifferent. Species suffer directly from grazing and trampling, but they may also suffer indirectly from the altered salinity and compression of the soil. The species which were most consistently and negatively influenced by grazing in these grasslands were *Filipendula ulmaria, Galium palustre, Lathyrus palustris, Pedicularis palustris, Phragmites australis, Rhinanthus serotinus*, and *Vicia cracca*. In contrary, the abundances of *Agrostis stolonifera, Carex nigra, Festuca rubra, Juncus gerardii, Leontodon autumnalis, Poa subcaerulea, Potentilla anserina*, and *Trifolium repens* were increased by grazing (Jutila 1999a).

The well-known fact that grazing decreases the abundance of common reed was obvious in the results: the dense and monotypic hydrolittoral reed stands were only found in the ungrazed plots. *Phragmites australis* was a very characteristic species also in the geolittoral and in the transition zone of the ungrazed transects. Instead the *Eleocharis uniglumis–Carex mackenziei* community and *Agrostis stolonifera* stands were observed only in the grazed hydrolittoral plots. This community-type, like some other shore communities favoured by grazing, are not particularly rich in species, but can have some infrequent species. Mud-flat annuals, which often colonise grazed hydrolittorals, were also found in the pastures, outside the plots. In many cases, trees invade to the upper parts of the ungrazed shore meadows and lead to forested epilittoral. Thus, largest epilittoral meadows are found in grazed areas. The ordination results indicated that both grazed and ungrazed areas have some unique features. Because grazed areas nowadays make up only a small percentage of the shores along the Baltic, traditional grazing management will increase the habitat diversity of an area. Cattle grazing has been proved to be effective in conserving certain bird communities and rare species.

There does not exist a single optimal management scenario for all coastal meadows. Management and restoration are dependent on the aims of nature conservation; whether the goal is to save meadow bird species, meadow plant communities, individual plant species, species richness, certain habitat types or even open coastal landscape. The stocking rate suitable for conservation purposes depends on the local conditions, habitat type, herbivore species etc. As a rule of thumb can be suggested in boreal seashore meadows 1 cattle/ha and in delta 2 cattle/ha during summer.

Acknowledgements

I thank Prof. Jim Grace and my supervisor Prof. Heikki Toivonen, for advice and comments on this manuscript. Many thanks to those who helped with the field work and data storage. The work was funded by grants from the Kone Foundation and the Academy of Finland.

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