Vascular plant species richness in grazed and ungrazed coastal meadows, SW Finland

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The richness of vascular plant species in four grazed and five ungrazed shore meadow communities was studied on the west coast of Finland, near the town of Pori (61°30´–61°33´N, 21°28´–21°41´E). In the transects established, plant species were studied in 412 1-m^2 plots and in the adjacent areas. The flora included a total of 183 vascular plant species representing 108 genera. The shore plant communities were dominated by perennial monocot species, although the number of dicot species was higher. The vascular plant species richness (11.5 ± 4.7) in 1-m^2 sample plots was significantly higher at the seashore than in the delta of the river Kokemäenjoki. A model is constructed of the factors that affect species richness in seashore meadows. Species richness increased significantly with increasing distance from the waterline, and more importantly ($R^2 = 0.26$) with elevation above the mean sea level. The linear increase in species richness continues up to a certain elevation, the latter being dependent on the amplitude of water level fluctuation. Species richness decreased significantly with an increase in biomass or height of vegetation. These variables are negatively correlated with elevation and have only secondary importance for species richness. In the delta area no significant results were obtained for species richness in general. The vascular plant species richness was higher in grazed plots than in ungrazed ones in the delta, but in the transects most exposed by the sea the opposite was true. The influence of grazing on the species richness seemed to be scale-dependent.

Key words: biomass, ecology, grassland, grazing, management, plant species richness, vegetation, water level fluctuation

INTRODUCTION

The plant species richness of a given area depends on evolutionary and historical factors, such as speciation and migration (Whittaker 1977, Taylor *et al.* 1990, Cornell & Lawton 1992), and on eco-logical factors, such as competition, disturbance, stress, successional state, herbivory and regeneration (Grubb 1977, Grime 1979, Huston 1979). These factors operate on different time and regional scales (Shmida & Wilson 1985, Zobel 1992, Eriksson 1993). It has been claimed that

species richness is highest at intermediate levels of disturbance (Huston 1979) and productivity (Al-Mufti *et al.* 1977, Shipley *et al.* 1991), but numerous studies have shown the complexity of such relationships (Moore & Keddy 1989, van der Maarel & Titlyanova 1989, Wisheu & Keddy 1989, Gough *et al.* 1994). There exists an extensive literature concerning the effects of grazing on grassland communities (Bakker 1978, Fresco *et al.* 1987, Gibson *et al.* 1987, Chaneton & Facelli 1991, Smith & Rushton 1994), however, studies of the acidic grasslands of the boreal zone are few.

In the boreal zone, for instance in Finland, most meadows are seminatural; natural grasslands exist only in the uplifting coastal zone, adjacent to flooding rivers and lakeshores, and on some cliffs, mountains and mires. Traditionally, large areas of seashore meadows and islands were grazed or mown, but after the 1940s management almost ceased and the shore landscape changed considerably, since the stands of the common reed (*Phragmites australis*) expanded heavily in many shore meadows. Changes in landscape, plant communities and bird fauna were quickly recognized, but were rarely thoroughly studied (Kauppi 1967, Tyler 1969, Soikkeli & Salo 1979, Ulfvens 1991). Due to the occurrence of a number of other changes in shore communities during this century (eutrophication, summer-cottage building, decrease in winter ice coverage and its duration), the relative importance of the various factors is still somewhat vague.

There is a longstanding tradition of Finnish research concerning the Baltic seashore meadow vegetation, for instance on the coast and islands of the Gulf of Bothnia (e.g. Leiviskä 1908, Siira 1970, Vartiainen 1988), on the coast of the Gulf of Finland (e.g. Häyrén 1902, Brenner 1921, Fagerström 1954, Buch 1959) and on the Archipelago Sea (e.g. Lemberg 1933, Palmgren 1961). There has also been research in Sweden (e.g. Tyler 1969, Ericson & Wallentinus 1979, Ericson 1981, Jerling 1983, Cramer & Hytteborn 1987) and in Estonia (e.g. Lippmaa 1934, Rebassoo 1975). These surveys, however, were mainly descriptive, and the focus was rarely on species richness (Palmgren 1925, Valovirta 1937, Palomäki 1964, Vartiainen 1980). The Finnish studies have concentrated on the northern part of the Gulf of Bothnia, the Bothnian Bay, and only few studies and in-

ventories of seashore vegetation have been carried out in the southern part, the Bothnian Sea (Häyrén 1909, Vaahtoranta 1964).

I studied the vegetation in grazed and ungrazed coastal meadows on the shore of the Bothnian Sea. The hypothesis was that the species richness increases with increasing elevation above sea level and that it is affected by grazing. I first surveyed the average and cumulative vascular plant species richness in different sample scales in four grazed and five ungrazed shore meadows embracing several vegetation zones. I then related environmental parameters to species richness and constructed a model of vascular plant species richness in the coastal meadows. I also tested whether stresses (water level fluctuation, salinity) and disturbances (grazing) affect species richness as predicted by Grime (1979) and Gough *et al.* (1994). The annual species were compared with perennial ones and monocots with dicots.

MATERIAL AND METHODS

Study area and sites

The study area is situated on the western coast of Finland, by the Bothnian Sea, near the town of Pori (61°30´–61°33´N, 21°28´–21°41´E). Four grazed and five ungrazed shore meadows, two of them in the delta area (transects G4 and UG4) of the river Kokemäenjoki and the rest by the sea, were investigated in 1993 and 1994 (Jutila 1994). The grazed areas are nationally valuable as traditional agricultural areas (Jutila *et al.* 1996). The meadows are important for avifauna, and have other conservational values as well. The number of sites that could be selected for this study was limited by the availability of grazed meadow areas.

The annual mean temperature, precipitation and the average duration of snow cover for the study area is + 4.3°C (– 6.5°C in January, + 16.0°C in July), 536 mm (22 mm February, 75 mm August), and 94 days, respectively (Finnish Meteorological Station Service). The sea at the Mäntyluoto station is frozen over for an average of 95 days (Seinä & Peltola 1991). Although the Baltic Sea does not have regular tides, seasonal and daily fluctuations in the water level are important factors affecting shore vegetation. In the growing season the water level usually fluctuates within 20-cm limits, but changes of up to one meter can occur. In winter the fluctuation is wider. The study area belongs to the southern boreal zone. The bedrock is predominantly Jotnian sandstone, with occasional olivine diabase intrusions.

In spring 1993, basic investigation transects (Fig. 1) were established for four grazed meadows (Kuuminainen (G1), Pihlavaluoto (G2), Eteläranta (G3) and Fleiviiki (G4))
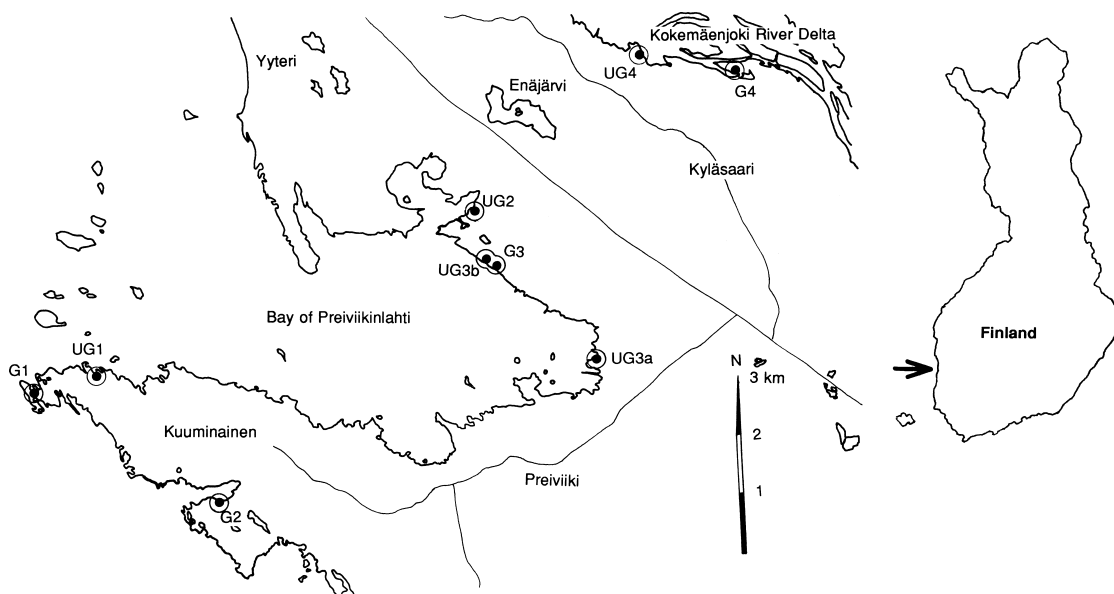
Fig. 1. Study sites in Pori, Finland. (Drawn by Karri Jutila.)

and four ungrazed ones (Hevoskari (UG1), Riitsarka (UG2), Paarnoori (UG3a) and Teemuluoto (UG4)). One new ungrazed transect (Vertailu-Eteläranta, UG3b) was established in 1994.

Methods

The beginning of each transect was established at the point where the emergent vegetation began, i.e. approximately at the average summer level of the sea. The transects ran perpendicularly from the shore to the forest, through 3–5 vegetation zones, which were numbered in the same direction. Sampling points were identified by the distance (measured along the transect) from the beginning of the transect and by the right-angled distance from the transect to the sampling place.

Plant communities were described within randomized plots for each vegetation zone. In July, August and September 1993, a total of 217 1-m^2 plots, located along all transects except UG3b, were studied. In 1994, an additional 195 1-m^2 plots were described for transects G1 and UG1, for one vegetation zone in the delta area (transects G4 and UG4) and for two vegetation zones in transects G3 and UG3b. The percentage cover of each vascular plant species was estimated in the plots. Species were further subdivided into monocotyledons, dicotyledons and pteridophytes and, according to life-history types, into trees and herbaceous species, which were further divided into annuals, biennials and perennials (modified according to Hämet-Ahti *et al.* 1988, which the scientific nomenclature also follows). Annuals are known to be indicators of disturbance. The division into mono- and dicots is pertinent because it corresponds to life-

form groups: nearly all monocots in these environments are graminoids (grasses, sedges and rushes). In 1994, the average height of the vegetation was measured in 165 0.25-m^2 plots (within the 1-m^2 plots). The adjacent vegetation of all the transects (within 20 m on each side) was thoroughly studied in order to obtain a more extensive list of the vascular plant species in the study areas.

In August 1993 and 1994, the total above-ground biomass (including living and dead material) was harvested from 0.5×0.5-m^2 plots located within the 1-m^2 vegetation plots. The biomass samples were weighed to the nearest 0.001 g, either the same day (1994) or the next day (1993, when the samples were preserved in a cold room) to determine their fresh weight. The samples were then dried at 60°C for one day and weighed again. Some samples collected in 1994 decayed when waiting for species identification; their dry weight was calculated using a coefficient (= dry weight/fresh weight).

The depth of the organic layer was measured from the seed bank samples gathered in the spring of 1993 and 1994. The soil type was determined: (1) visually on the basis of seed bank samples, and (2) on the basis of soil map information. The first method yielded six types, numbered according to diminishing grain size: gravel, sand, fine sand, silt, clay and peat. The second method yielded the five categories of till, sand, fine sand, silt and clay.

In 1994, the transects were leveled at intervals of 5 meters with an altimeter. Using the water-level data of the Finnish Institute of Marine Research station at Mäntyluoto, the profiles of the transects were drawn. The elevation of each plot was linearly interpolated from the values measured in the transect, and the influence of perpendicular distance from the transects was ignored.

Fig. 2. Vascular plant species in whole flora of transects, divided into systematic (bar front) and life-history groups (bar side).

Fig. 3. Vascular plant species in 1-m² plots, divided into systematic (bar front) and life-history groups (bar side).

Statistical analyses

Statistical analyses were performed using the Statistical Analysis System, SAS (Anon. 1988) and the normality of all the variables were tested. I ran different tests for the whole data and divided it into groups such as riverside vs. seashore, grazed vs. ungrazed, seashore grazed vs. seashore ungrazed, transect pairs, transects etc.

I used multi- and univariate regression analyses to study the dependence of the vascular plant species richness on the distance from the waterline (the beginning of the transect), elevation above sea level, dry and fresh biomass, height of vegetation, and depth of organic layer. There was no difference in the results of univariate regression using log-transformed biomass ($\log_{10}(x + 1)$) and actual biomass values. No other transformations were performed. The environmental variables used in the regressions were all parametric. I first performed univariate regressions; this allowed the use of a larger number of samples than in multivariate regressions, where the data were restricted by the variable with the smallest sample number. The high correlation between explanatory variables (parametric, Pearson, and nonparametric Kendall, correlation analysis) also forced me to use univariate regression, in addition to multivariate, to ensure the validity of the results. I used linear multivariate regressions and also fitted some nonlinear regressions to the data.

Covariance analysis was used to test the difference in species richness between grazed and ungrazed areas, but significant interactions restricted the use of some results. A pairwise *t*-test was used to test the differences in the number of monocot vs. dicot species and annual vs. perennial species. ANOVA (procedure GLM in SAS) was used to test the difference in average species richness between delta and seashore sites and between different vegetation zones.

RESULTS

Total flora

A total of 183 vascular plant species, representing 108 genera, were found in the study areas (Appendix). The species included 65 monocots (29 genera), 110 dicots (72 genera), 3 gymnosperms (3 genera) and 5 ferns (4 genera) (Fig. 2). The 1-m² sample plots (*n* = 412) contained a total of 144 species, which can be divided into 48 monocot, 91 dicot, 3 gymnosperm and 2 fern species (Fig. 3). The sampling thus covered 78.7% of the flora.

The total numbers of species (including all species within 10 m distance from the transect) in various transects are presented in Fig. 2. The

cumulative species richness in the grazed and un-grazed plots is plotted separately against eleva-tion in Fig. 4. Cumulative species richness in-creases more quickly in ungrazed than in grazed areas, but eventually both reach the same level.

The studied meadows are dominated by per-ennial monocots (163 species). Annuals are quite few, only 20 species in total and 14 in the plots. They were not found at all in transect UG4 and only two were observed in transect G4. The rich-est annual flora was found in the grazed transect G1, with 15 annual species, of which nine occurred also in the plots. Transect G2 had six annual spe-cies, all of them also in the plots (Figs. 2 and 3).

Species richness in plots

On an average, 11.5 ± 4.7 vascular plant species were found in the 1-m^2 sample plots. In the delta area the number of species (< 10) was significantly (0.001) lower than by the shore (> 10 species). This was consistent for monocots, dicots, annu-als as well as perennials. Transect UG1 had on average the richest flora (14.4 ± 4.4). The species numbers on individual plots varied from one to 25; the richest plots were found in UG1, UG2, and G3. Analysis of variance showed a signifi-cant difference in species numbers between the vegetation zones ($F = 49.4^{***}$), indicating an in-crease in species richness in vegetation zones situ-ated at higher elevations above sea level.

The pairwise *t*-test showed that in the plots of the whole data there were significantly more per-ennial species than annuals ($T = 51.7$) — also for the transects separately — and more dicot spe-cies than monocots ($T = 5.5$). The prevalence of dicotyledon species was not significant in all tran-sects, and in G4 there was a prevalence of mono-cots. Nevertheless, the monocots were clearly more abundant than the dicots.

Environmental and related parameters affect-ing species richness in the study plots

There were significant and fairly strong correla-tions between the environmental variables. For instance, elevation above sea level was correlated, positively or negatively, with most of the other
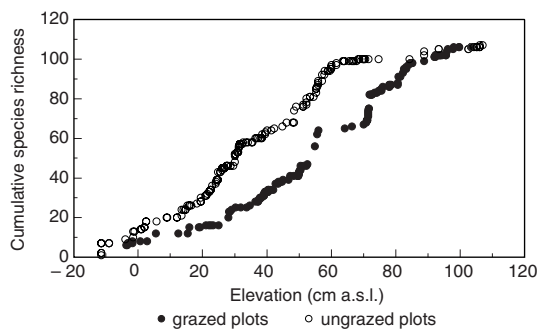
Fig. 4. Cumulative species richness plotted against the elevation for grazed and ungrazed 1-m^2 seashore plots.

variables (Table 1). The correlations were much weaker in the river delta area than by the sea.

The univariate categorical regression indicates that the soil type did not significantly affect the species richness. It was dependent on the vegeta-tion zone ordering, but the regression was weaker than between elevation above sea level and spe-cies richness (Table 1).

Species richness along the elevation gradient

Species richness increased significantly with in-creasing elevation above the mean sea level (Fig. 5). The linear relationship was fairly strong for the whole data ($R^2 = 0.25$), and even stronger in the ungrazed plots ($R^2 = 0.36$) and the ungrazed sea-shore plots ($R^2 = 0.34$). In transect G2, the eleva-tion explained up to 77% of the species richness. There was no such relationship in the delta area (Table 2). In all transects by the seashore the re-gression was significant (Fig. 6). Above a certain elevation, species richness became level or began to decrease (Fig. 7). Second order exponential function revealed an R^2 value of over 0.30 for the whole data.

Elevation and distance from the waterline showed a strong positive correlation. Elevation generally explained more of the variation in spe-cies richness than distance from the beginning of the transect, but this was not so in the transects G1, UG1, G2 and UG3a.

Dicot species richness increased at higher ele-vations, but the number of monocots remained almost the same from the sea level to over 1 m

Fig. 5. Regression of species richness divided into monocot and dicot species in seashore data.

elevation. Thus dicot species were even more strongly dependent on elevation than vascular plant species in general (Fig. 5). The few ferns and trees were respectively encountered only in the plots higher than 40 and 50 cm above sea level. The number of annual species was highest at intermediate elevations, i.e. in drift deposits.

Species richness and biomass

The species richness in the plots was significantly negatively correlated with fresh and dry biomass

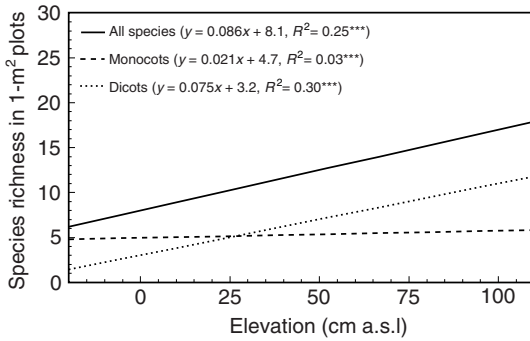Table 1. Correlation matrix of the explanatory variables based on 1 m^2 data. DB = distance from beginning of transect, Elev. = elevation, Fresh = fresh weight of biomass, Dry = dry weight of biomass, Veg. height = height of vegetation, Zone = ordering number of vegetation zone (water → forest), Zone length = length of vegetation zone, DOL = depth of organic layer, PMT = soil type from a map (1–6 from coarse to fine and organic).

	Elev.	Fresh	Dry	Veg. height	Zone	Zone length	DOL	PMT
DB	0.33037[a]	− 0.1202[a]	− 0.0975[a]	− 0.2664[a]	0.40789[c]	0.18549[b]	0.00826[a]	0.18803[c]
P <	0.0001	0.0231	0.0620	0.0005	0.0	0.0001	n.s.	0.0001
N	411	357	367	165	411	411	398	406
Elev.		− 0.4625[a]	− 0.3658[a]	− 0.5636[a]	0.64071[c]	− 0.2202[b]	− 0.0748[a]	− 0.2462[c]
P <		0.0001	0.0001	0.0001	0.0	0.0001	n.s.	0.0001
N		357	367	165	411	411	398	406
Fresh			0.9500[a]	0.73618[a]	− 0.3080[c]	0.08591[b]	0.16341[b]	0.16195[c]
P <			0.0001	0.0001	0.0001	0.0201	0.0001	0.0001
N			354	162	357	357	348	355
Dry				0.71962[a]	− 0.2074[c]	0.05449[b]	0.11222[b]	0.07673[c]
P <				0.0001	0.0001	n.s.	0.0024	0.0518
N				148	367	367	358	365
Veg. height					− 0.2432[a]	0.0103[b]	0.15699[b]	0.31487[c]
P <					0.0001	n.s.	0.0059	0.0001
N					165	165	161	165
Zone						− 0.25435[c]	0.03841[c]	− 0.02101[c]
P <						0.0001	n.s.	n.s.
N						411	398	406
Zone length							0.03299[c]	0.25273[c]
P <							n.s.	0.0001
N							398	406
Depth of organic layer								0.11108[c]
P <								0.0047
N								398

[a] = Pearson correlation coefficient

[b] = Nonparametric Kendall's correlation coefficient, when variation of variable(s) was not normal or when parametric correlation was not significant.

[c] = Nonparametric Kendall's correlation coefficient, when at least the other variable was nonparametric.

Table 2. Multivariate and univariate regression analysis of vascular plant species richness based on 1-m^2 plot data. Pr.E. = parameter estimate.

Data and pre-dictor variables	N	Pr.E.	S.D.	R^2	Cumulative P<	N	Pr.E.	S.D.	R^2	Cumulative P<	N	Pr.E.	S.D.	R^2	Cumulative P<
Whole data															
Unimodel	411				0.0001										
Intercept		7.808	0.368		0.0001										
Elevation		0.009	0.007	0.253	0.0001										
Multimodel	358				0.0001	145				0.0001	148				0.0001
Intercept		7.429	0.744		0.0001		8.695	1.420		0.0001		11.51	1.059		0.0001
Elevation		0.075	0.008	0.246	0.0001		0.061	0.013	0.253	0.0001		0.047	0.014	0.274	0.0011
Dry weight		−0.013	0.004	0.264	0.0023		−0.022	0.006	0.318	0.0006		−0.010	0.008	0.312	0.2132
DOL		0.361	0.100	0.290	0.0004		0.434	0.162	0.352	0.0081					
Height of veg.												−0.023	0.009	0.339	0.0151
Seashore															
Unimodel	321				0.0001										
Intercept		8.144	0.454		0.0001										
Elevation		0.086	0.008	0.255	0.0001										
Multimodel	286				0.0001	125				0.0001					
Intercept		7.993	0.927		0.0001		15.61	1.175		0.0001					
Elevation		0.070	0.009	0.241	0.0001		0.010	0.014	0.233	0.4843					
Dry weight		−0.018	0.005	0.279	0.0002		−0.024	0.008	0.391	0.0017					
DOL		0.425	0.121	0.309	0.0005										
Height of veg.							−0.030	0.009	0.444	0.0009					
Delta															
Unimodel	91				0.4266										
Intercept		8.712	0.483		0.0001										
Elevation		0.011	0.014	0.001	0.4266										
Multimodel	72				0.3336	23				0.3866					
Intercept		9.097	1.161		0.0001		2.160	3.717		0.5680					
Elevation		0.018	0.020	0.015	0.3520		0.139	0.088	0.074	0.1322					
Dry weight		0.009	0.012	0.017	0.4315		0.012	0.029	0.133	0.6935					
DOL		−0.191	0.128	0.048	0.1404										
Height of veg.							0.027	0.027	0.144	0.6221					
Grazed															
Unimodel	201				0.0001										
Intercept		7.062	0.554		0.0001										
Elevation		0.078	0.010	0.250	0.0001										
Multimodel	152				0.0001	43				0.0018					
Intercept		6.349	1.027		0.0001		5.201	1.738		0.0048					
Elevation		0.078	0.011	0.286	0.0001		0.052	0.021	0.205	0.0168					
Dry weight		−0.002	0.007	0.286	0.7296		0.011	0.012	0.199	0.3376					
DOL		0.136	0.135	0.290	0.3168										
Height of veg.							0.108	0.042	0.317	0.0133					
Ungrazed															
Unimodel	210				0.0001										
Intercept		7.846	0.469		0.0001										
Elevation		0.112	0.010	0.356	0.0001										
Multimodel	190				0.0001	105				0.0001					
Intercept		10.48	1.107		0.0001		12.50	1.039		0.0001					
Elevation		0.089	0.011	0.357	0.0001		0.075	0.016	0.470	0.0001					
Dry weight		−0.028	0.005	0.444	0.0001		−0.020	0.008	0.569	0.0136					
DOL		0.146	0.135	0.448	0.2786										
Height of veg.							−0.023	0.010	0.591	0.0220					

(Continues …)

Table 2. Continued.

Data and pre-dictor variables	N	Pr.E.	S.D.	Cumulative R^2	Cumulative $P<$	N	Pr.E.	S.D.	Cumulative R^2	Cumulative $P<$	N	Pr.E.	S.D.	Cumulative R^2	Cumulative $P<$
Seashore grazed															
Unimodel	146				0.0001										
Intercept		6.594	0.750		0.0001										
Elevation		0.090	0.012	0.279	0.0001										
Multimodel	124				0.0001	33				0.0607					
Intercept		5.808	1.192		0.0001		6.482	4.837		0.1906					
Elevation		0.082	0.012	0.280	0.0001		0.039	0.046	0.164	0.4143					
Dry weight		− 0.005	0.008	0.283	0.4877		0.003	0.025	0.203	0.8947					
DOL		0.231	0.168	0.294	0.1706										
Height of veg.							0.122	0.048	0.221	0.0171					
Seashore ungrazed															
Unimodel	174				0.0001										
Intercept		8.468	0.544		0.0001										
Elevation		0.106	0.011	0.339	0.0001										
Multimodel	162				0.0001	92				0.0001					
Intercept		11.17	1.217		0.0001		15.14	1.014		0.0001					
Elevation		0.076	0.011	0.342	0.0001		0.048	0.014	0.595	0.0014					
Dry weight		− 0.034	0.006	0.477	0.0001		− 0.025	0.007	0.643	0.0005					
DOL		0.279	0.151	0.488	0.0673										
Height of veg.							− 0.030	0.009	0.684	0.0010					

(Fig. 8). The decrease in species number was evident in ungrazed transects (Table 2). A weak negative regression was also found in some grazed transects (G2 and G3), but not in the whole data from them. Dry biomass (when both measured and calculated values were used, but not with measured values alone) explained the variation in species richness better than fresh weight, although for the whole data the R^2 was quite low (0.2). The variation explained was higher for the seashore data, and was actually over 50% for the ungrazed seashore data. The decrease in species richness with an increase in standing crop was more evident for dicots than for monocots, but the explained variation in dicots was even lower than for the vascular plant species on average.

Fresh and dry weights were highly significantly and positively correlated. The weights were negatively correlated with the distance from the beginning of the transect and even more clearly with elevation (Table 1).

Species richness and height of vegetation

Species richness decreased significantly with an increase in the height of the vegetation (measured only in 1994); the variation explained was 24%

for the data as a whole. The height of the vegetation was highly significantly correlated with the distance from the beginning of the transect, with the elevation, as well as with the weight variables (Table 1). Elevation best explained the variation in vegetation height.

Species richness and the depth of the organic layer

There was a weak but significant linear regression between the depth of the organic layer and species richness in the whole data, the seashore data and the data from the ungrazed plots (Table 2). In fact, this regression seemed to be of a nonlinear, hump-shaped type, with the highest species richness at an intermediate level of the soil organic layer.

Multivariate regression models

The linear multivariate regression models with the best fit included elevation, dry weight, depth of organic layer and height of vegetation (Table 2). In the delta area no multivariate model studied was significant. Elevation explained 20–50% of the variation in the different data sets. The height
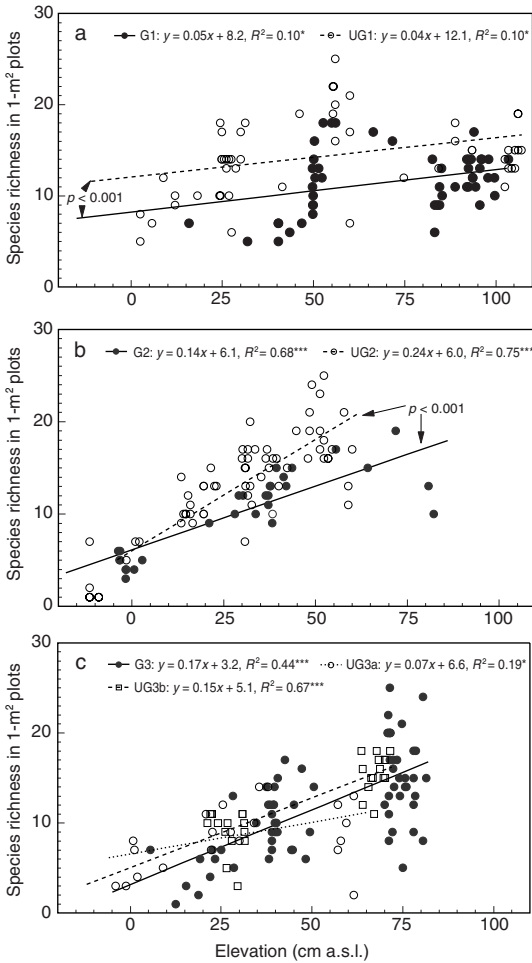
Fig. 6. Regression of the vascular plant species richness in 1-m² plots against elevation in the seashore transects: a) G1 and UG1, b) G2 and UG2, and c) G3, UG3a and UG3b. The significance of covariance analysis is indicated with *p*-values.

Fig. 7. Regression of vascular plant species richness in 1-m² plots against elevation in all seashore transects. — a: Below 70 cm elevation. — b. Above 70 cm elevation.

of vegetation seemed to be quite an important explanatory variable in those samples where it was measured ($N = 148$), and in some models it actually accounted for more of the species richness than elevation. Since the dry biomass was correlated with the height of vegetation and had a weaker correlation with species richness, when used in the same model it was no longer a significant factor.

Different multivariate models explained species richness in the grazed and ungrazed areas (Table 2). At the grazed sites, elevation was usually the only significant explanatory variable.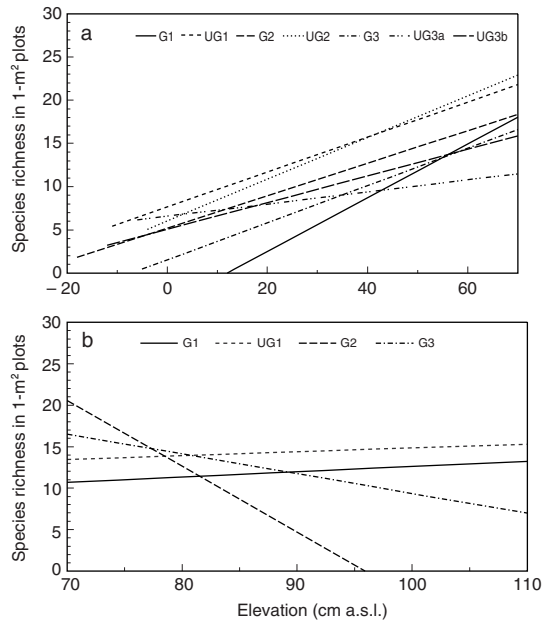 The effect of dry biomass and depth of the organic layer were insignificant, but the height of vegetation was a significant variable, which raised the R^2 to 31% (Table 2).
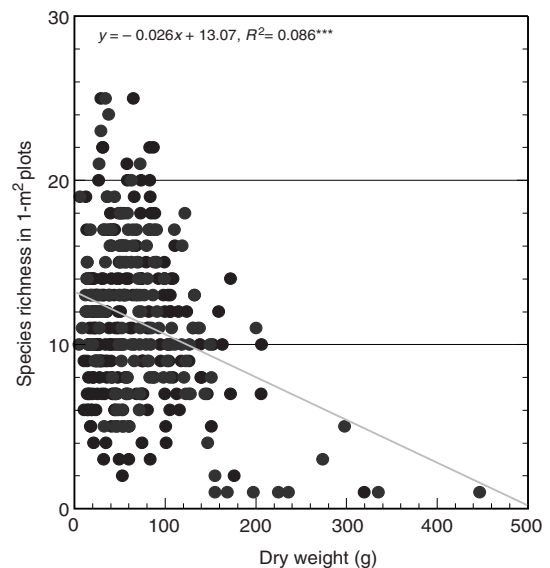

Fig. 8. Species richness in 1-m² plots against dry weight of biomass.

In the ungrazed plots much more of the species richness was explained ($R^2 = 0.59$) by dry biomass, height of vegetation and elevation than in the grazed plots. At the seashore, the depth of the organic layer was a significant variable in the species richness model (Table 2).

Species richness in grazed and ungrazed areas

The difference in the species richness between grazed and ungrazed plots was tested with covariance analysis (elevation as a covariate). Significant positive interactions between elevation and grazing in the covariance analysis prohibited a valid use of some results, e.g. those for the whole data. At the seashore, the species richness was significantly higher in the ungrazed than in the grazed plots. This holds for dicots, biennials and perennials, but not for monocots (Table 3). In the delta, the species richness of all species, monocots and perennials, but not of biennials, was significantly higher in the grazed than in the ungrazed plots.

Since different transect pairs were at different elevations it was necessary to analyse them separately. Also the effect of grazing was studied in several elevation groups (< 20 cm, 20–50 cm, 50–70 cm and > 70 cm). When the seashore data was divided to transect pairs and elevation groups, it was evident that in most elevation groups dicots and pteriophytes were negatively affected by grazing (Table 3). Significant regression between grazing and elevation somewhat confused the pattern. The number of biennial species was reduced by grazing at low elevations, but at higher elevations it seemed to increase (Table 3).

DISCUSSION

General species richness

In the delta there were fewer vascular plant species than at the seashore, owing to differences in location and environmental conditions (e.g. fresh vs. saline water, differences in flooding, different soil composition). The flooding of nutrient-rich river water renders the delta meadows productive habitats, dominated by a few perennial monocots.

The absence of annuals indicates that flood is more of a periodical stress than a serious disturbance. In the ungrazed area the accumulation of litter and taller vegetation reduces the availability of light, with a negative effect on species richness (Tilman 1993). Competition, which is severe in productive habitats (Grime 1979), may be one reason for species poverty.

At the seashore, fluctuation in the water level, together with erosive forces such as waves, ice and wind, affect plant communities directly and indirectly (Cramer & Hytteborn 1987). For example, they create competition-free gaps and affect the coarseness and holding capacity of water and nutrients. The seashore is a stress-disturbance environment, where the significance of disturbance depends on the degree of exposure. The seashore transects in this study present a fairly wide variation in the disturbance gradient. The transects richest in species, dicots and annuals (on the basis of the whole flora) are G1 and UG1, which are situated by the open sea and are most severely affected by the destructive forces. At midsummer and at the end of summer the shores blossom with annuals and biennials, such as *Odontites litoralis*, *Rhinanthus serotinus*, *Centaurium* spp. and *Linum catharticum*, indicative of disturbances. Due to climatic and geological factors, such as the ice age, acidic bedrock and soil composition, the species pool is smaller in my study area than for instance in the calcareous seashore meadows of Estonia (cf. Rebassoo 1975).

Effects of elevation and distance from the waterline on species richness

In seashore meadows the pattern of species richness is dependent on dynamic processes, both short-term fluctuations in the sea level and long-term changes (primary succession) due to land uplift (Vartiainen 1980), which is also constantly modifying local habitat conditions to a considerable extent (Zobel & Kont 1992). The unstable vegetation zonation resulting from this, with ecoclines and spatial variation in relation to other environmental conditions such as topography, substrate and degree of exposure, has led to a high beta diversity and to the development of vegetation classifications with many syntaxa (Vartiainen

1980, Toivonen & Leivo 1993, Pykälä *et al.* 1994). At the Baltic shores, species richness can be seen as induced by the combined influence of habitat

diversity and a mass effect (Schmida & Wilson 1985).

Species richness is lowest at the waterline, since only a few stress-tolerant species (often

Table 3. Covariance analysis of vascular plant species richness with elevation as covariate and grazing as class variable. Transect pairs are compared. Because of significant interaction between explanatory variables, the whole data could not tested with covariance analysis. *N* = number of plots. The number of grazed/ungrazed plots is in parentheses. *P* > indicates significance with the whole transect pair data. Richer shows if the grazed (G) or ungrazed (U) transect has higher species richness in 1-m² plots. Elevation groups shows the results of covariance analysis in elevation groups, which are in seashore and transects G1 and UG1: < 20 cm, 20–50 cm, 50–70 cm and > 70 cm and in delta and other transect pairs < 20 cm, 20–50 cm and > 50 cm. Capitals indicate significant results. * = There is significant interaction between grazing and elevation, a = plots only in G4.

Data	N		P <	Richer	Elevation groups
All species					
Delta (G4 vs. UG4)	91	(55/36)	0.0087	G	g, g, gᵃ
Seashore	320	(146/174)	0.0001	U	U*, U*, u, u
G1 vs. UG1	104	(51/53)	0.0001	U	u, U, U* ,U
G2 vs. UG2	97	(28/69)	0.0001	U*	u, U, g
G3 vs. UG3a + UG3b	119	(67/53)	0.3560	u	u, u, u
Monocots					
Delta (G4 vs. UG4)	91	(55/36)	0.0037	G	G, g, gᵃ
Seashore	320	(146/174)	0.0764	g	g*, u, G, g*
G1 vs. UG1	104	(51/53)	0.0122	U	u, U, g, u
G2 vs. UG2	97	(28/69)	0.4420	g*	g, u, g
G3 vs. UG3a + UG3b	119	(67/53)	0.0003	G	u, g, G*
Dicots					
Delta (G4 vs. UG4)	91	(55/36)	0.1914	g	g, g, gᵃ
Seashore	320	(146/174)	0.0001	U	U*, U*, U, U
G1 vs. UG1	104	(51/53)	0.0001	U	u, U, U*, U
G2 vs. UG2	97	(28/69)	0.0001	U*	U, U, g
G3 vs. UG3a + UG3b	119	(67/53)	0.0007	U	g, U, u
Pteridophytes					
Delta (G4 vs. UG4)	91	(55/36)	0.1872	u	u, u, gᵃ
Seashore	320	(146/174)	0.0001	U*	–, U*, U*, U*
G1 vs. UG1	104	(51/53)	0.0064	U	–, u, U, –
G2 vs. UG2	97	(28/69)	0.0288	U*	–, u, u
G3 vs. UG3a + UG3b	119	(67/53)	0.0215	U	–, –, U
Annuals					
Delta (G4 vs. UG4)	91	(55/36)	0.1433	g*	g, g, gᵃ
Seashore	320	(146/174)	0.0019	U*	u, U, u, U
G1 vs. UG1	104	(51/53)	0.2498	u	u, u, u, u
G2 vs. UG2	97	(28/69)	0.0174	U*	u, u, U
G3 vs. UG3a + UGb	119	(67/53)	0.3762	u	–, u, U*
Biennials					
Delta (G4 vs. UG4)	91	(55/36)	0.1433	u	u, u, –
Seashore	320	(146/174)	0.0046	U	U, U, u*, G
G1 vs. UG1	104	(51/53)	0.7807	u	u, u, g, G
G2 vs. UG2	97	(28/69)	0.0001	U	u, U, –
G3 vs. UG3a + UGb	119	(67/53)	0.0001	U	u, U, g
Perennials					
Delta (G4 vs. UG4)	91	(55/36)	0.0098	G	g, g, gᵃ
Seashore	320	(146/174)	0.0001	U	U*, U*, u, u
G1 vs. UG1	104	(51/53)	0.0001	U	u, U, U, U
G2 vs. UG2	97	(28/69)	0.0003	U*	u, U, g
G3 vs. UG3a + UG3b	119	(67/53)	0.3879	u	u, u, u

graminoids) can thrive in this harsh environment (stress-inducing waves, ice and brackish water); in other words the 'potential species richness' (Gough *et al.* 1994) is low. On the most wind-exposed, coarse-grained shores, only few vascular plant species survive. In more sheltered places, where finer-grained soil material has accummulated, meadows can develop. Tall stands with a considerable standing crop can develop in the hydro- and lower geolitoral, species-poor communities. In the middle and upper geolitoral, communities consisting mostly of graminoids are invaded by herbs. Species richness is usually at its highest in the transition zone of the geo- and epilitoral. The increase in species richness by the Baltic Sea, with the distance from waterline and with elevation, has been noted by many botanists (Palmgren 1925, Valovirta 1937, Palomäki 1964, Vartiainen 1980), but the phenomenon has not been studied in any particular scale. Autti (1993) has used 1-m^2 plots sampled systematically every three meters on the Bothnian Bay; her results agree with mine.

The relationship between species richness and elevation above mean sea level is linear to a certain elevation level (Vartiainen 1980), which is determined mainly by water level fluctuation. In the Pori area this level is 60–70 cm above the sea (Fig. 7a and b). Higher up other environmental factors, such as soil and management, begin to play a significant role. Elevation is actually a multivariate and indirect parameter encompassing the effect of various stress or disturbance factors, such as surface and ground water level, waves, ice and salinity, on seashore habitat conditions. Nevertheless elevation, as an accurately measurable parameter, can be a practical indicator of species richness for conservation and management in coastal meadows.

In some transects (G1, UG1 and UG3a) species richness was more strongly dependent on distance from the waterline than on elevation. This may be due to the steep inclination and maritime location of transects G1 and UG1: distance from the waterline assures a better escape than mere elevation from the influence of waves, storms and salt-water spray. In the long transect UG3a, the inclination is very flat and fluctuating, resulting in different conditions (for instance in the pH) at the same elevation both near the waterline and near the forest fringe (e.g. Siira 1970).

Species richness, biomass and height of vegetation

The results for the ungrazed seashore transects represent (Fig. 8) the decreasing part of the normal curve (Al-Mufti *et al.* 1977) between dry biomass and species richness and are in agreement with other studies (Moore & Keddy 1989, Wisheu & Keddy 1989, Garcia *et al.* 1993). The maximum species richness occurred with dry weights of 116, 137 and 259 g/m^2; these findings are comparable to those obtained in lakeshore studies in Canada (Wisheu & Keddy 1989). In the grazed areas only a weak negative regression between the above-ground biomass and species richness was found, which can be seen as a sign of low grazing intensity. In the ungrazed sites the decreasing regression was highly significant.

Height of vegetation seemed to be quite a good indicator of species richness. There was a significant negative regression, which was understandably most evident in the ungrazed transects, but was also found in many grazed transects.

As vegetation-related parameters, both height and biomass were highly significantly and negatively correlated with elevation, i.e. they were dependent on elevation-bound stress and disturbance factors. The rest of the variation in species richness explained by height or biomass alone (not in combination with elevation) may be related to soil fertility. On the basis of the ungrazed sites it can be roughly estimated that, of the variation accounted for, the contribution of elevation was 80% and that of height + biomass 20%. As an indicator of stress, elevation defines 'the potential richness', to which biomass, height of vegetation and competitive exclusion contribute to produce 'realized richness' (Gough *et al.* 1994).

One exception to the trend of decreasing biomass with increasing species richness in shore meadows has often been seen in the vegetation of drift deposits, established at the upper limit of seasonal sea water fluctuation. In these deposits, both the biomass and the species number are relatively high.

Species richness, soil material and organic layer

The type of soil did not predict species richness in the plots. Shore meadows are always some-

what sheltered, and the soil is always relatively small grained. In more exposed sites the grain size would be bigger and the vegetation more patchy. It is thus not surprising that in other studies the soil grain size has been found to be related to species richness (Vartiainen 1988).

The depth of the organic layer in these uplifting seashore areas is quite low. Species richness seems first to increase with the depth of the organic layer, but after a certain limit the trend turns downward. In my study sites, the selection procedure restricted epilitoral sites mainly to dry areas, which may have contributed to the decrease in species richness at higher elevations.

Effect of grazing

The covariance analysis of the investigated transect pairs revealed contradictory results. In the river delta area, the vascular plant, monocot and perennial species richness was higher in the grazed meadow than in the ungrazed one, both in the plots and in the whole flora of the transects. Comparable results have been reported in mesotrophic grassland pastures (Smith & Rushton 1994) and in mown wet meadow communities (Mueller *et al.* 1992, Kotanska 1993). Higher standing crop, taller vegetation and a smaller number of annuals indicates more shading, moister conditions and maybe more competition in UG4 than in G4. In transect UG4, bushes, mainly *Salix phylicifolia,* grow at fairly low elevations and the deciduous forest fringe is relatively close to the waterline. If grazing ceased, bushes would soon expand in the meadow (already as dwarf saplings). In the pasture of Fleiviiki (elsewhere than in the transect), there are also halophytes as relicts of the influence of saline water, and other rare species that are not found in the ungrazed areas.

It was observed that, at the seashore, species richness was higher in the ungrazed plots than the grazed ones. The result is inconsistent with that of Kauppi (1967) and Bakker (1987, 1989), but conforms better to the results of Chaneton and Facelli (1991) and Rawes (1981). Similarly, dicot species richness was higher in the ungrazed plots than in the grazed ones. This is opposite to the findings of Bullock *et al.* (1994). It might be argued that the grazing pressure was inappropriately

low (Pandey & Singh 1991) or high. The present results could also mean that while in seminatural meadows grazing increases species richness, this does not hold for natural grassland communities in the boreal zone, represented for example by the Baltic seashore meadows.

According to Tyler (1969), most of the seashore species are negatively affected by grazing, although the most frequent species seem rather indifferent. That was the result also in this study, monocots (e.g. graminoids) being the most frequent species. The pattern of the cumulative species richness curve (Fig. 4) would suggest that grazing reduces species richness in the geolitoral and increases it in the epilitoral. A similar trend was clear in the number of biennial species (Table 3).

I think that the results concerning the effect of grazing are scale-dependent. This conclusion can be drawn when we compare the species richness in the whole flora of the sites (hectares) and that of the individual plots (1 m^2). For example, in transects G1 and UG1, almost the same number of species was observed in the whole flora (100 and 99, respectively), and there was no clear difference between the grazed and ungrazed flora. The same applies to transects G2 and UG2 with 81 and 85 species, respectively. The flora in the grazed sites is evidently not species-poorer or species-richer than in the ungrazed sites, but the vegetation pattern is more coarse-grained (de Pablo *et al.* 1982, Gibson *et al.* 1987, Rescia *et al.* 1994). If an even larger unit area were studied, the result might be the reverse, in favour of grazed areas; more importantly, it should be noted that weaker competitors and rare species seem to benefit from grazing (Gibson *et al.* 1987).

When species richness was compared in the plots and in the whole flora of transects G3 and controls UG3a and UG3b, there was no clear difference. This may be due to the fact that in the Eteläranta area (transect G3) the last grazing period, at the end of the growing season, has continued for only five years and grazing has mainly affected the epilitoral vegetation.

In the whole flora there were more annual species in the grazed than in the ungrazed areas. In addition to natural gaps, cattle trampling also creates gaps which can be invaded by ephemerals. All such gaps are not quickly invaded because of overly dry conditions or high salinity levels. Af-
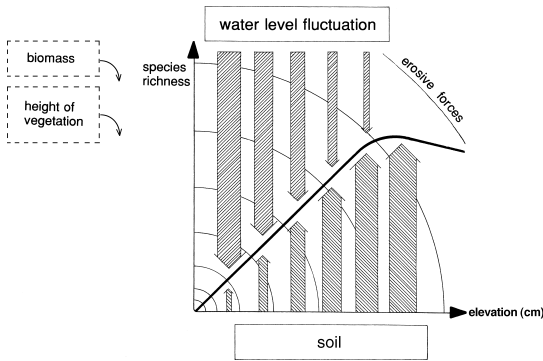
Fig. 9. General model of vascular plant species richness in seashore meadows and the effect of important variables. Species richness (y-axis) (in a fairly small unit area) increases with increasing elevation (x-axis). This is mainly due to fluctuation in the water level, a stress factor, which is greatest at the water line and decreases with elevation (the arrows become smaller). Similarly the frequency and intensity of erosive forces (disturbance factor) decreases with elevation and affects species richness. The influence of the soil (fertility, structure etc.) becomes increasingly important with elevation; above a certain elevation it becomes the primary factor affecting species richness. In the shore community, biomass and height of vegetation are influenced by stress and disturbance factors, and their negative relationship with species richness is thus merely secondary.

ter long-lasting grazing, litoral plant communities are quite different from ungrazed ones.

Provided that the soil is suitable, *Phragmites australis* usually produces dense and monocultural stands at the waterline, where species richness is in any case low, and in a narrow fringe between the geo- and the epilitoral, where it forms tall relict, senescent stands (Tyler 1969). The geolitoral reed stands are very conspicuous, but sparser and species richer than hydrolitoral stands. *Phragmites australis* may survive further up in the zonation in ungrazed shore meadows, but it suffers from grazing in grazed soils (Tyler 1969).

General model

In shore communities, species richness is mainly dependent on the stress and disturbances caused by fluctuating water (Fig. 9). The scale, regularity and seasonality of fluctuations, the duration and intensity of the disturbances, and the soil type,

which is largely dependent on the erosive forces, select from the local species pool such species that are able to endure the harsh waterline conditions. At higher elevations (and perhaps also at lower ones, for instance under water), stress and disturbances have less effect on the plant communities, and other factors, such as the fertility of the soil, species competition, light availability and management, begin to determine species richness.

Grazing reduces species richness, at least on a small scale, at the seashore and increases it in the delta. Grazing seems to narrow the transition areas between vegetation zones, where due to the mass effect species diversity is higher than in the surroundings. Grazing eliminates some species, it narrows the realized amplitude of the distribution of others species, and it creates opportunities for new species to arrive. The vegetation pattern in grazed areas is coarser. It seems evident that natural disturbance at the waterline, combined with grazing disturbance, raises the species richness/ elevation curve to higher elevations. In this model, biomass has no primary effect. It is negatively correlated with elevation and thus also negatively correlated with species richness.

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Appendix. All species in plots (P) and in whole flora of transects (X). Per. = perennial, ann. = annual, bien. = biennial.

	G1	UG1	G2	UG2	G3	UG3a	UG3b	G4	UG4	Life-history type
Achillea millefolium	PX	PX	–	–	–	–	X	X	–	Per.
A. ptarmica	–	–	–	–	PX	P	–	–	–	Per.
Acorus calamus	–	–	–	–	–	–	–	X	–	Per.
Agrostis canina	–	–	X	–	–	–	–	P	P	Per.
A. capillaris	PX	PX	PX	PX	PX	–	PX	P	–	Per.
A. gigantea	X	PX		PX	PX	(P)	PX	–	–	Per.
A. stolonifera	PX	PX	PX	PX	PX	P	PX	P	P	Per.
Alisma plantago-aquatica	–	–	–	X	–	–	–	–	P	Per.
Alnus glutinosa	X	PX	X	X	PX	X	PX	–	–	Per. tree
A. incana	–	–	–	–	P	–	X	–	–	Per. tree
Angelica sylvestris	X	PX	X	PX	PX	P	PX	–	–	Per.
Anthoxanthum odoratum	P	PX	PX	P	X	–	X	P	–	Per.
Arabidopsis thaliana	P	–	–	–	–	–	–	–	–	Ann.

(Continues …)

Appendix. Continued.

	G1	UG1	G2	UG2	G3	UG3a	UG3b	G4	UG4	Life-history type
Artemisia vulgaris	–	PX	–	–	–	–	–	–	–	Per.
Atriplex longipes	PX	–	–	–	–	–	–	–	–	Ann.
A. prostrata	P	–	–	–	PX	–	–	–	–	Ann.
Betula pendula	–	X	–	P	–	–	X	–	–	Per. tree
B. pubescens	–	X	–	–	–	–	–	P	–	Per. tree
Calamagrostis arundinacea	–	–	P	–	–	–	–	–	–	Per.
C. epigejos	PX	P	–	P	–	–	–	–	–	Per.
C. stricta	PX	PX	PX	PX	PX	P	PX	P	P	Per.
Caltha palustris	–	PX	–	PX	PX	–	PX	P	P	Per.
Cardamine hirsuta	X	–	–	–	–	–	–	–	–	Ann.
C. pratensis	–	–	–	PX	–	P	X	P	P	Per.
Carex aquatilis	–	–	–	–	–	–	–	P	P	Per.
C. canescens	–	–	–	–	–	–	–	P	P	Per.
C. disticha	–	–	–	–	–	–	–	–	X	Per.
C. glareosa	–	–	P	PX	PX	P	–	–	–	Per.
C. mackenziei	–	P	PX	–	P	P	PX	–	–	Per.
C. nigra	PX	PX	PX	PX	PX	–	PX	P	P	Per.
C. panicea	–	P	–	P	–	–	–	–	–	Per.
C. rostrata	–	–	–	–	–	–	–	–	P	Per.
C. serotina	–	–	PX	–	X	–	–	–	–	Per.
C. vesicaria	–	–	–	–	–	–	P	–	X	Per.
Centaurium littorale	–	PX	X	–	X	–	–	–	–	Bien.
C. pulchellum	–	P	P	–	–	–	–	–	–	Ann.
Cerastium fontanum	PX	–	PX	P	PX	P	PX	X	–	Per.
Ceratophyllum demersum	–	–	–	–	–	–	–	–	X	Per.
Chenopodium album	–	PX	–	–	–	–	X	–	–	Ann.
Cicuta virosa	–	–	–	–	–	–	–	P	P	Per.
Cirsium arvense	PX	–	–	X	–	–	–	–	–	Per.
C. palustre	–	–	X	P	–	P	–	–	–	Bien. or per.
Dactylorhiza incarnata	–	X	–	–	–	–	–	–	–	Per.
Danthonia decumbens	–	PX	PX	PX	–	–	–	P	–	Per.
Deschampsia bottnica	X	–	–	–	–	–	–	–	–	Per.
D. caespitosa	–	–	PX	PX	PX	P	PX	P	–	Per.
D. flexuosa	PX	PX	P	–	X	P	X	X	–	Per.
Dryopteris carthusiana	–	–	X	–	–	–	–	–	–	Per.
Eleocharis acicularis	X	–	–	–	X	–	–	–	–	Per.
E. palustris	–	–	–	–	–	–	–	P	P	Per.
E. parvula	X	X	–	–	–	–	X	–	–	Per.
E. quinqueflora	P	–	–	X	PX	–	–	–	–	Per.
E. uniglumis	PX	PX	PX	PX	PX	P	PX	–	–	Per.
Elymus arenarius	X	–	–	–	–	–	–	–	–	Per.
E. caninus	X	–	P	–	–	P	–	–	–	Per.
E. repens	PX	PX	PX	P	P	P	X	–	–	Per.
Empetrum nigrum	–	–	–	PX	X	–	X	–	–	Per. dwarf shrub
Epilobium angustifolium	PX	–	–	–	X	–	X	–	–	Per.
E. palustre	–	–	–	PX			PX	P	P	Per.
Equisetum arvense	–	X	–	–	–	–	–	–	–	Per. pteridophyta
E. fluviatile	–	–	–	–	–	–	–	P	P	Per. pteridophyta
Eriophorum angustifolium	–	–	X	–	P	–	PX	P	–	Per.
Erysimum hieraciifolium	X	–	–	–	–	–	–	–	–	Bien.
Euphrasia stricta	P	P	–	PX	–	–	X	P	–	Ann.
Festuca arundinacea	P	PX	PX	PX	PX	–	PX	P	–	Per.
F. ovina	P	–	–	–	–	–	–	P	–	Per.
F. rubra	PX	PX	PX	PX	PX	P	PX	P	–	Per.
Filipendula ulmaria	PX	PX	PX	PX	PX	P	PX	P	P	Per.
Fragaria vesca	PX	PX	–	–	X	–	X	–	–	Per.
Galeopsis bifida	P	P	–	PX	PX	–	–	–	–	Ann.
G. speciosa	–	–	–	P	–	–	–	–	–	Ann.

(Continues …)

Appendix. Continued.

	G1	UG1	G2	UG2	G3	UG3a	UG3b	G4	UG4	Life-history type
Galium palustre	PX	PX	PX	PX	PX	P	PX	P	P	Per.
G. trifidum	X	–	–	P	PX	–	PX	–	–	Per.
G. uliginosum	X	PX	X	PX	–	–	–	–	–	Per.
G. verum	PX	PX	–	–	–	–	–	–	–	Per.
Geum rivale	X	P	PX	–	P	–	–	–	–	Per.
Glaux maritima	PX	PX	PX	–	PX	P	X	–	–	Per.
Hieracium umbellatum	–	PX	–	X	–	–	–	–	–	Per.
Hierochloë odorata	–	–	–	–	P	P	PX	–	–	Per.
Hippophaë rhamnoides	PX	P	X	–	–	–	–	–	–	Per. bush
Hippuris vulgaris	–	–	–	–	–	–	–	X	–	Per.
Iris pseudacorus	–	–	–	–	–	–	–	–	P	Per.
Juncus alpinoarticulatus	–	PX	X	X	PX	–	P	–	–	Per.
J. articulatus	–	–	P	–	–	–	–	–	–	Per.
J. balticus	–	X	–	–	–	–	–	–	–	Per.
J. bufonius	X	–	X	X	X	–	–	–	–	Ann.
J. filiformis	–	P	–	–	–	P	–	P	–	Per.
J. gerardii	PX	PX	PX	PX	PX	P	PX	X	–	Per.
J. ranarius	X	–	–	–	–	–	–	–	–	Ann.
Juniperus communis	P	X	X	PX	X	–	X	X	–	Per. tree
Lathyrus palustris	X	P	–	PX	PX	P	PX	P	X	Per.
L. pratensis	–	–	P	–	P	–	P	P	–	Per.
Leontodon autumnalis	PX	PX	PX	PX	PX	–	X	P	–	Per.
Linaria vulgaris	PX	PX	–	–	X	–	–	–	–	Per.
Luzula multiflora	X	X	–	PX	P	–	P	P	–	Per.
L. pilosa	–	P	–	–	–	–	–	X	–	Per.
Lycopodium annotinum	–	–	X	–	–	–	–	–	–	Per.
Lycopus europaeus	–	X	X	–	–	–	–	–	–	Per.
Lysimachia thyrsiflora	–	–	X	PX	PX	–	PX	P	P	Per.
L. vulgaris	X	X	–	P	P	P	PX	X	–	Per.
Lythrum salicaria	–	X	X	P	–	–	–	–	P	Per.
Maianthemum bifolium	–	P	P	–	–	P	–	–	–	Per.
Melica nutans	–	X	X	–	–	–	–	–	–	Per.
Milium effusum	X	P	P	–	–	X	–	–	–	Per.
Montia fontana	–	–	–	P	–	–	PX	P	–	Ann.
Myosotis laxa	–	–	–	PX	–	–	–	–	–	Ann. or bien.
M. stricta	X	–	–	–	–	–	–	–	–	Ann.
Myrica gale	–	X	–	X	–	–	–	–	–	Per. bush
Nardus stricta	–	–	–	–	–	–	–	P	–	Per.
Odontites litoralis	PX	P	PX	PX	PX	P	X	–	–	Ann.
Ophioglossum vulgatum	X	PX	P	PX	PX	–	PX	–	–	Per.
Oxalis acetosella	–	–	X	–	–	–	–	–	–	Per.
Parnassia palustris	PX	PX	X	PX	PX	P	PX	–	–	Per.
Pedicularis palustris	X	PX	–	PX	PX	P	PX	–	–	Bien.
Peucedanum palustre	X	X	–	PX	PX	P	PX	–	P	Bien.
Phalaris arundinacea	–	X	–	X	–	–	–	–	–	Per.
Phleum pratense	X	–	–	X	P	–	–	–	–	Per.
Phragmites australis	P	PX	PX	PX	PX	P	PX	P	P	Per.
Picea abies	X	X	X	P	X	–	X	–	–	Per. tree
Pinus sylvestris	X	X	X	PX	PX	–	P	–	–	Per. tree
Plantago major	PX	–	–	–	–	–	–	–	–	Per.
P. maritima	PX	PX	PX	X	PX	X	X	–	–	Per.
Poa angustifolia	–	–	–	–	–	–	X	–	–	Per.
P. nemoralis	–	X	–	–	–	–	–	–	–	Per.
P. pratensis	–	PX	P?	–	–	–	–	–	–	Per.
Poa subcaerulea	PX	P	X	PX	PX	–	X	P	–	Per.
Polygonum aviculare	PX	–	–	–	–	–	–	–	–	Ann.
P. lapathifolium	X	–	–	–	–	–	–	–	–	Ann.
Potamogeton pectinatus	–	X	–	–	–	–	–	–	–	Per.

(Continues …)

Appendix. Continued.

	G1	UG1	G2	UG2	G3	UG3a	UG3b	G4	UG4	Life-history type
Potentilla anserina	PX	PX	PX	PX	PX	P	PX	P	–	Per.
P. argentea	PX	–	–	–	–	–	–	–	–	Bien. or per.
P. erecta	–	X	–	PX	X	–	–	P	–	Per.
P. palustris	–	X	X	PX	PX	–	X	P	P	Per.
Prunella vulgaris	–	PX	X	–	–	–	–	–	–	Per.
Prunus padus	X	–	–	–	–	–	–	–	–	Per. tree
Puccinellia distans	X	–	–	–	–	–	–	–	–	Per.
Ranunculus acris	PX	PX	PX	PX	PX	–	PX	P	–	Per.
R. repens	–	–	P	–	P	–	–	–	–	Per.
Rhinanthus serotinus	PX	PX	–	PX	PX	P	PX	–	–	Ann.
Ribes alpinum	X	–	X	–	–	–	–	–	–	Per. bush
R. spicatum	X	X	P	–	–	–	–	–	–	Per. bush
Rosa dumalis	X	–	X	–	–	–	–	–	–	Per. bush
R. rugosa	X	–	–	–	–	–	–	–	–	Per. bush
Rubus arcticus	–	X	–	–	–	–	–	–	–	Per.
R. idaeus	PX	PX	P	X	–	P	X	–	–	Per. bush
R. saxatilis	–	P	X	–	–	–	–	–	–	Per.
Rumex acetosa	PX	PX	P	PX	X	–	PX	–	–	Per.
R. acetosella	PX	–	P	–	–	–	–	P	–	Per.
R. crispus	PX	–	–	PX	X	–	P	–	–	Per.
R. hydrolapathifolium	–	–	–	–	–	–	–	–	P	Per.
Sagina nodosa	–	P	X	X	–	–	–	–	–	Per.
S. procumbens	PX	–	–	X	PX	–	–	–	–	Per.
Salix phylicifolia	–	X	–	X	–	P	X	P	P	Per. bush
S. repens	–	–	–	–	–	–	–	X	–	Per. dwarf shrub
Schoenoplectus lacustris	–	–	–	–	–	–	–	–	X	Per.
S. tabernaemontani	X	PX	PX	PX	P	P	X	–	–	Per.
Scutellaria galericulata	–	–	–	X	–	–	–	–	–	Per.
Sedum acre	PX	–	–	–	–	–	–	–	–	Per.
S. telephium	PX	–	–	–	–	–	–	–	–	Per.
Silene dioica	–	–	P	–	–	–	–	–	–	Per.
Sorbus aucuparia	X	X	PX	–	–	P	–	–	–	Per. tree
Spergularia salina	X	–	–	–	–	–	–	–	–	Ann. or bien.
Stellaria graminea	PX	PX	–	P	–	–	PX	–	–	Per.
S. palustris	–	–	–	PX	–	P	–	P	P	Per.
Tanacetum vulgare	P	X	–	–	–	–	–	–	–	Per.
Taraxacum	PX	PX	PX	–	–	–	–	–	–	Per.
Trientalis europaea	–	PX	P	X	X	P	X	–	–	Per.
Triglochin maritimum	PX	PX	PX	PX	PX	P	PX	–	–	Per.
T. palustre	PX	PX	X	PX	PX	P	PX	P	P	Per.
Trifolium pratense	P	X	–	–	PX	–	PX	–	–	Per.
T. repens	PX	PX	PX	PX	PX	–	PX	P	–	Per.
Typha latifolia	–	–	–	PX	–	–	–	–	–	Per.
Urtica dioica	X	P	–	–	–	–	–	–	–	Per.
Vaccinium myrtillus	–	–	–	–	–	–	–	P	–	Per.
Valeriana sambucifolia	P	PX	X	PX	PX	P	PX	–	–	Per.
Veronica chamaedrys	PX	PX	–	P	–	–	–	X	–	Per.
V. officinalis	PX	–	–	–	–	–	–	–	–	Per.
V. scutellata	–	–	–	–	–	–	X	–	–	Per.
Vicia cracca	X	PX	–	PX	PX	P	PX	–	–	Per.
Viola canina	X	PX	PX	PX	X	–	–	–	–	Per.
V. palustris	–	P	P	PX	X	P	–	P	–	Per.
V. riviniana	–	–	X	–	–	–	–	–	–	Per.
V. tricolor	P	–	–	–	–	–	–	–	–	Ann. or per.