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The vascular plant flora of shell gravel deposits on the Åland Islands, SW Finland — community structure in relation to calcium

Ralf Carlsson[1)], Carl-Adam Hæggström[2)] and Patrik Kraufvelin[3)4)]

[1)] *Husö Biological Station, AX-22220 Emkarby, Åland, Finland (correspondence address: Högbackagatan 10, AX-22100 Mariehamn, Åland, Finland, e-mail: ralf.carlsson@lyceum.ax)*
[2)] *Finnish Museum of Natural History, Botanical Museum, P.O. Box 7, FI-00014 University of Helsinki, Finland*
[3)] *Environmental and Marine Biology, Åbo Akademi University, Akademigatan 1, FI-20500 Åbo, Finland*
[4)] *ARONIA, Coastal Research Team, Raseborgsvägen 9, FI-10600 Ekenäs, Finland*

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Plants are referred to as calciphilic (calcicole) or acidophilic depending on their relation to lime. We censused the vascular plant flora on seven shell gravel deposits from the Littorina Age and in two reference areas with naturally high species richness on the Åland Islands, assuming that a higher proportion of calciphilic plants would be found on the shell gravel deposits than elsewhere. Both the total number of plants and the number of calciphiles showed a significant positive correlation with the calcium (Ca) concentrations of the soils, but the highest number of species and proportions of calciphilic species were not found on shell gravel, but at intermediate to high Ca-levels in areas affected by man and domestic animals. We did not observe a strong influence of Ca on the species distribution patterns, otherwise than possibly indirectly via a raised pH-value. On the contrary, the strongest explanatory environmental variable seemed to be phosphorus, P. This in turn raises further questions: Should we rather use the word alkaliphilic? Are plants Ca-dependent or Ca-tolerant? Could the whole story be about P and not Ca? When switching the analytical focus from sites to species, Ca-neutral species were on average found at more sites than moderately or strongly calciphilic species. In a species-based ordination, the calciphiles also clustered significantly differently from the Ca-neutral species, both when analysing all species simultaneously and when analysing a subset of the most widely distributed species. The exact meaning of this is hard to evaluate, but it may give a hint that many calciphiles could be poor generalists and that the Ca concentration not always was sufficiently high at all shell-gravel sites. It also demonstrates the functionality of dividing species into these four groups with regard to Ca dependency, especially if the Ca-neutral group solely consists of acidophilic species. This is also in support for a continuing use of calciphilic plants as indicators for rough assessments or initial screenings of plant diversity in applied conservation.

Introduction

In many floras (e.g. Niering *et al.* 1983, Mossberg *et al.* 1992) plants are referred to by the vaguely defined words calciphilic (calcicole) or acidophilic or that they prefer lime or acidic soils, respectively (e.g. Niering *et al.* 1983). There are also many studies on plants and their relation to calcium (e.g. Jefferies & Willis 1964, Führer 2005, Rodwell *et al.* 2007). In Finland, Eklund (1946) divided plants into different groups according to their relation to lime. These groups were strictly limestone-dependent (German: *kalkstet*), strongly calciphilic (*stark kalkhold*) and moderately calciphilic (*kalkbegünstigt*). From a large material and literature studies, Eklund (1946) noted that some species grew only in limestone areas or where the till had a high content of lime so he made the assessment that some plants were exclusively associated with these areas, others to a smaller degree and some not at all.

The bedrock of the Åland Islands consists of different varieties of acidic rapakivi granite, with an age of about 1580 Ma (Bergman 1981, Suominen 1991). The soils of the Åland Islands are, contrary to the Finnish mainland, in many places, mixed with limestone of Ordovician origin from the bottom of the Bothnian Sea, deposited during the last ice age (Hausen 1964). Another source of lime is shell gravel. Shell gravel deposits have been known for a long time on the Åland Islands and were used as means for soil improvement (Brenner 1927). Few investigations of the flora on shell gravel are known from Finland (e.g. Olsoni 1943). In Sweden, the flora on shell gravel from the Littorina Age was investigated by Halden (1920, 1921). Hallberg (1971) studied the vascular plant flora on shell gravel on the Swedish west coast. One of the authors (RC) has studied the shell gravel deposits from a geological point of view (Carlsson 2002, 2003) and in connection with field work noted that the vascular plant flora on the deposits sometimes contained rare species.

To further investigate the botany of shell gravel deposits, we (1) censused the vegetation at seven shell gravel sites and at two other areas, (2) counted the number of species, (3) evaluated the proportion of calciphilic species, and (4) tried to find out which factors may govern the species composition of these deposits by relating species composition to environmental variables. One hypothesis was that a larger proportion of calciphilic plants would be found on shell gravel than elsewhere (Eklund 1946). Another hypothesis was that high concentrations of calcium might be inhibitory to plants and low levels would not be sufficient for the calciphilic plants. If so, the distribution of plants in relation to calcium would follow the optimum curve and thus the intermediate disturbance hypothesis (Connell 1978). Finally, we wanted to check for possible relationships between species and registered environmental variables at specific areas as well as possible similarities in distribution over areas for species belonging to the same group with regard to Ca dependency. A clarification of these questions should be of direct benefit in applied conservation, since at least the most Ca-dependent species may serve as indicators, giving a hint as to what other species may be found and specific nature-protection values of certain areas.

Material and methods

We visited seven sites on shell gravel (Hulta, Knutsboda, Tengsöda, Brännbolstad, Dånö, Högbolstad, Stålsby) and two reference areas (Bovik and Markusböle) in the middle of July in 2003 or 2004 and May 2005 (Fig. 1). We recorded all vascular plants growing at the shell-gravel sites. Based on Eklund (1946), we divided the plants into four groups: Ca-neutral (0), moderately calciphilic (1), strongly calciphilic (2) and Ca-dependent (3). According to our experience *Anemone ranunculoides*, *Dactylorhiza fuchsii*, *Rosa mollis* and *R. sherardii* are calciphilic, hence here they were treated as such. It is worth mentioning that at the time of Eklund *D. fuchsii* was not even considered a separate species but it was included in *D. maculata*. The vegetation of the reference areas was lush, but to our knowledge these areas were not affected by or associated with lime from shell gravel. Instead they were on flat ground that has risen above sea level during the last few hundred years or so.

In September and October 2004, we took soil samples (0.5 l) from the uppermost layer of the mineral soil from the shell-gravel sites and in October 2005 from the reference sites. Subsamples of 15 ml were extracted for one hour in a solution of 150 ml acid ammonium acetate (pH 4.65) and analysed for exchangeable Ca^{2+}, PO_4^-, K^+ and Mg^{2+}, determined by atomic absorbtion spectrometry at the laboratory of the Agri- and Horticultural Research Station of the Åland Islands. Subsamples of 25 ml of dried, ground soil were mixed with 62.5 ml of ion-exchanged water and pH and was measured after 17 hours. NO_3^- was measured on moist soil potentiometrically.

Since the shell gravel deposits may be regarded as islands in the landscape, we calculated the species-area relationship according to the following formula: $S = CA^z$ or in a logarithmic form $\log S = z\log A + \log C$, where S is the actual number of species on the island, A is the area of the island and C is a constant, denoting the y-intercept, giving the species number on one unit of island area. Theoretically, z should equal about 0.25 (MacArthur and Wilson 1967). We measured the areas of the investigated sites on a digital map (Map Source: Garmin). Finally, we compared the number of plant species with the calcium content of the soils. Since the areas of the investigated sites differed in size, we first calculated the average area of the sites and then transformed the number of species at each site to the number of species per average area.

For the data analysis we utilised both univariate and multivariate statistical techniques. We performed the univariate analyses with SYSTAT 11.01 and SPPS 13.0 (Sokal & Rohlf 1995) and the multivariate statistical analyses with PRIMER 6.0 (Clarke 1993). We first used an unbalanced one-way ANOVA to examine possible differences in the average numbers of sites where species from each of the four Ca-dependency groups were found. Due to heterogeneous variances this analysis was done on negatively inversely transformed data. Following a significant overall difference, Bonferroni-corrected pair-wise *a posteriori* test was performed. We then expressed presence or absence of each plant species at each site as 1 or 0, respectively, after which we compared the sites using multivariate statistical methods with PRIMER. Due to certain restrictive properties of the data (like a large

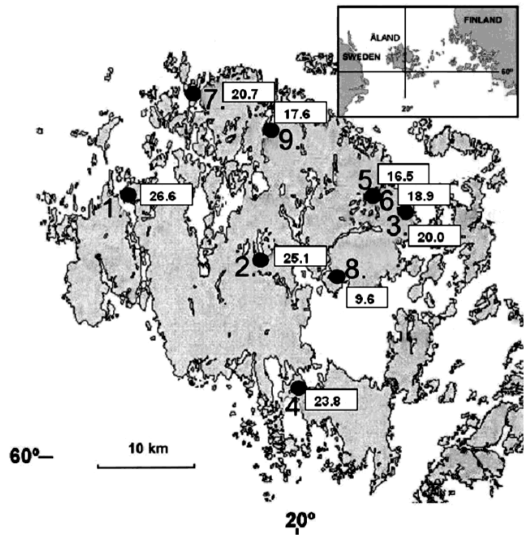

Fig. 1. The investigated area with sampling sites marked 1–9. The inserted numbers show the proportion of calciphilic plants at each site.

amount of zeros, the fact that most species were rare and that so few areas were investigated) we chose to use non-parametric multivariate techniques instead of corresponding parametric ones. We first applied non-metric multidimensional scaling (NMDS) combined with hierarchical agglomerative cluster analysis (group average method: Bray-Curtis similarities) on species data. To clarify the similarities between the shell gravel sites and to improve the possibilities for later matching the plant distribution patterns to environmental variables, we performed one set of NMDS ordination and cluster analysis on all plants and one set on calciphilic plants only. For an initial matching of environmental variables to biotic data, we applied a non-parametric Spearman correlation analysis, with which we tried to relate the number of species and the number of calciphiles to soil data as well as the soil variables to each other. The environmental variables were then analysed using the principal component analysis (PCA) and then subsequently combined with species data with the BIOENV procedure of the PRIMER software. BIOENV is capable of matching an environmental similarity matrix with a species similarity matrix using the Spearman coefficient and then to elucidate the best explanatory subset of environmental variables for a specific species distribution pattern (Clarke and Ainsworth 1993). To further investigate the actual environmental responses of the specific plant species and the four groups above with regard to Ca dependency (Eklund 1946), we conducted two NMDS ordinations on species instead of sites. First we analysed all species simultaneously and then we analysed a subset of the most widely distributed species (here using clearly acidophilic species as the Ca-neutral ones and representatives from all three levels of calciphilic species). The criteria for the inclusion of a specific species in this latter analysis (to keep the full objectivity in species selection) was that the Ca dependency was clearly defined and that the species was present in at least three (acidophilic species of group 0 and Ca-dependent of group 3) or four of the investigated areas (the moderately and strongly calciphilic species of groups 1 and 2, respectively). Finally, to clarify possible significant differences among the abovementioned four groups at the multivariate level, we performed two one-way analyses of similarity (ANOSIM), also with the aid of the PRIMER software.

Results

At the nine sites we found altogether 414 species (*see* Appendix). Of these, 118 could be regarded as more or less calcium-dependent according to Eklund (1946), 16 were strictly dependent, 52 strongly calciphilic, and 50 moderately calciphilic. These 118 species represented 28.5% of the total species richness and among the individual sites the proportion varied between 9.4% and 26.6% (mean ± SD = 20.1% ± 5.3%). The proportion of calciphiles generally decreased when going from west to east (Table 1 and Fig. 1). At one shell gravel site, Högbolstad (8), the number of calciphilic plants was remarkably low. On the contrary, at this site, there were several acidophilic species, e.g. *Carex canescens*, *Gnaphalium sylvaticum*, *Gnaphalium uliginosum*, *Juncus filiformis* and *Senecio sylvaticus*. Ca-neutral plants were generally more widely distributed than the calciphilic plants, for which the number of areas did not differ significantly (Fig. 2 and Table 2).

Species–area relationships were $S = 11.1A^{0.312}$

Table 1. Area, position according to the Finnish National Grid 27°E, and general description of the sites. Total number of plant species, total number of calciphiles, and numbers of calciphiles representing different groups based on their depency of Ca, observed at the sites. Ca^{+} = moderately calciphilic, Ca^{++} = strongly calciphilic, Ca^{+++} = Ca-dependent.

Site	Area (m^2)	Position	General description	Total	Calciphiles (% of total)	Ca^{+}	Ca^{++}	Ca^{+++}
1. Bovik	6000	6708-9:093-4	Wooded meadow and pasture.	232	62 (26.7)	26	26	10
2. Markusböle	6000	6699:108-9	Wooded meadow and pasture.	208	53 (25.5)	25	21	7
3. Hulta	1150	6704:126	Around irrigation pond; forest N, cultivated fields S.	94	19 (20.2)	9	6	4
4. Knutsboda	2900	6683:112	Two gravel pits separated by a road. Cultivated fields and forest. Wooded meadows in the past.	166	40 (24.1)	13	20	7
5. Tengsöda	5990	6706:122	Gravel pits, used as garbage dump. Forests and cultivated fields. Wooded meadows in the past.	185	31 (16.8)	16	13	2
6. Brännbolstad	8000	6705:122	Former wooded meadow, now summer house. Surrounded by coniferous forest and water.	120	23 (19.2)	9	13	1
7. Dånö	320	6720:102	Orchard and irrigation pond, surrounded by forest and fields. Possibly wooded meadows in the past.	138	29 (21)	10	17	2
8. Högbolstad	1875	6697:117-8	Three gravel pits, surrounded by mixed forest.	128	12 (9.4)	8	3	1
9. Stålsby	990	6714:111	Between a road and a forested hill. Cultivated fields west of the road.	85	15 (17.6)	8	7	0

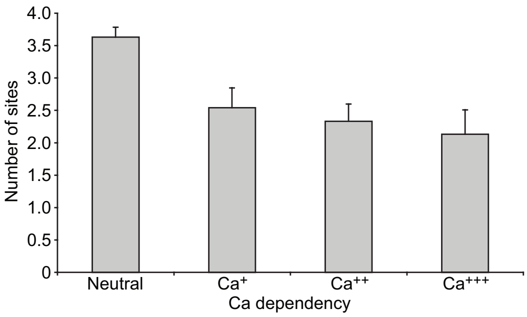

Fig. 2. Average numbers of sites (+ SE) where Ca-dependent species were present.

Table 2. One-way ANOVA and pair-wise comparisons on the number of sites where species representing the four groups based on their dependency of calcium were found. 0 = neutral species, 1 = moderately calciphilic species, 2 = strongly calciphilic species, 3 = strictly calcium dependent species. Overall difference: $F_{3,410}$ = 7.079***. * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$, ns = not significant.

	1	2	3
0	p = 0.022*	p = 0.002**	p = 0.226
1		p = 1.000	p = 1.000
2			p = 1.000

(p = 0.015, r^2 = 0.596) for all plants, and S_{calc} = $0.6A^{0.471}$ (p = 0.027, r^2 = 0.524) for calciphilic species, i.e. a faster rise in species number per unit area for calciphilic species than for all species.

There were rather high differences between the sites with regard to their species composition; the Bray-Curtis values were always higher for all plants than for calciphiles only (Table 3). Only 18 species were found at all nine sites (*see* Appendix). Of these, only *Tussilago farfara* was regarded as moderately calciphilic. Of the other 68 more or less common species found at 6–8 sites, only 9 were calciphilic: the lignose *Fraxinus excelsior*, the herbs *Filipendula vulgaris*, *Linum catharticum*, *Medicago lupulina*, *Mycelis muralis*, *Plantago lanceolata*, *Potentilla reptans* and *Ranunculus polyanthemos*, and the sedge *Carex digitata*. Species found at only one or two sites numbered 215, which is 51.9% of the total species pool.

The species found represented a wide spectrum of habitats: coniferous and deciduous woodlands, fens, wet, moist, mesic and dry meadows, rock outcrops, seashores, roadsides, gardens and ruderals habitats. A few rare

Table 3. Bray-Curtis similarities between the various sites with regard to species composition.

	Bovik	Markusböle	Stålsby	Dånö	Hulta	Högbolstad	Knutsboda	Tengsöda
All plants								
Bovik								
Markusböle	62.73							
Stålsby	37.85	42.32						
Dånö	45.41	44.51	46.64					
Hulta	45.40	52.98	45.81	44.83				
Högbolstad	45	45.83	38.50	47.37	42.34			
Knutsboda	57.29	57.75	46.22	57.89	55.38	52.38		
Tengsöda	57.55	58.02	53.33	60.68	53.05	54.31	67.81	
Brännbolstad	55.11	57.32	56.59	55.81	57.01	49.19	56.64	57.70
Calciphiles only								
Bovik								
Markusböle	53.91							
Stålsby	25.97	26.47						
Dånö	32.98	26.83	36.36					
Hulta	34.57	38.89	23.53	25				
Högbolstad	19.18	18.75	23.08	25	13.33			
Knutsboda	45.10	40.86	32.73	43.48	37.29	23.53		
Tengsöda	49.46	45.24	47.83	56.67	40	33.33	50.70	
Brännbolstad	44.71	42.11	42.11	38.46	33.33	35.29	38.10	51.85

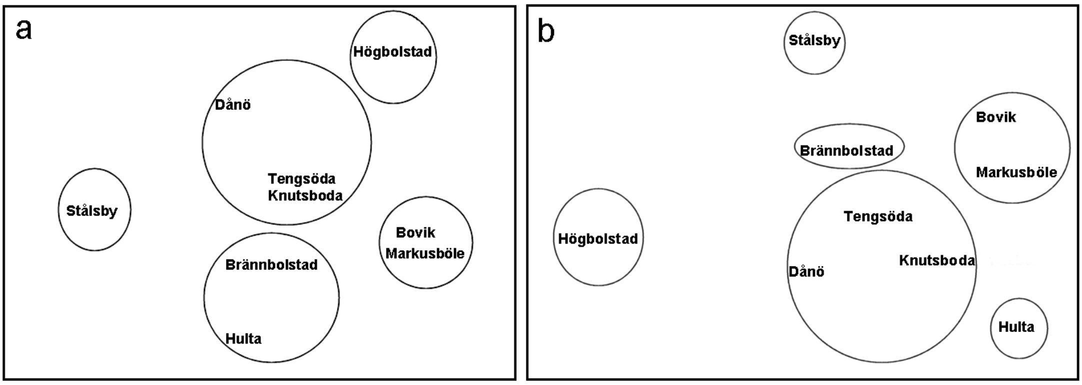

Fig. 3. NMDS ordination demonstrating the similarities/differences among the investigated sites with regard to the species content at each site: (**a**) all plants (circles superimposed at 55% Bray-Curtis similarity), (**b**) calciphiles only (circles superimposed at 45% Bray-Curtis similarity).

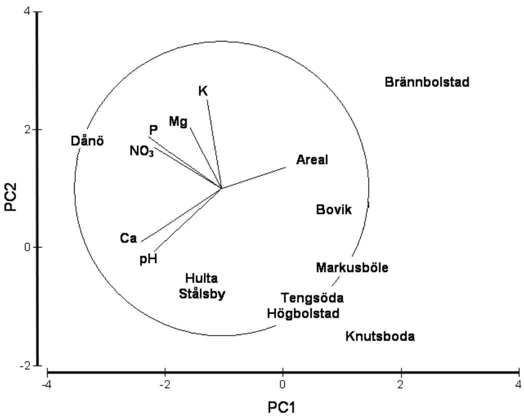

Fig. 4. PCA on environmental data (soil samples) from the investigated sites indicating where the various environmental variables had their highest values.

(Hæggström & Koistinen 1999) species such as *Blysmus compressus*, *Brachypodium sylvaticum*, *Cephalanthera longifolia*, *Equisetum variegatum*, *Gentianella amarella*, *Rosa sherardii*, *Samolus valerandi*, *Taxus baccata* and *Torilis japonica* were found.

When we clustered the sites according to presence/absence of all plants, the shell-gravel sites formed four distinguishable groups at 55% Bray-Curtis similarity, whereas the two reference sites clustered in a group of their own already at 62.7% Bray-Curtis similarity (Fig. 3a and Table 3). When only calciphilic plants were analysed, it was much harder to identify easily distinguishable groups with six groups at 45% Bray-Curtis similarity (Fig. 3b and Table 3).

Soil properties were highly variable, both between sites and within sites (Table 4). The mean ± S.D. for calcium at all sites was 24.6 ± 24.9 g l^{-1}. We found few significant correlations between our investigated variables (Table 5) except for calcium/pH. The correlation between calcium and number of species corrected for area was 0.750 ($p = 0.020$) and for calcium and corrected number of calciphiles 0.717 ($p = 0.030$).

A PCA on environmental data pointed out Dånö as a nutrient-rich area, and Dånö, Hulta and Stålsby as especially rich in Ca (Fig. 4). PC1 explained 44.9% of the variation in environmental data, whereas PC2 explained 27.1%. To our surprise, Ca was not included in the most important determinating variables of species distribution (Table 6). For all plants the most important environmental variables were P, pH and NO_3 (P alone most important), whereas for calciphiles the corresponding most important determinants were P, Mg and NO_3.

From the species-based NMDS-ordinations, visualising the distribution of species over sites, it is implied that most Ca-neutral species cluster in the upper parts of the ordination scheme, whereas the calciphiles mainly cluster in the lower parts (Fig. 5a), i.e. demonstrating some similarity in distribution with regard to Ca dependency (please note that the vast majority of the 414 species are overlapping in their distribution over sites and cannot therefore be made visible in the ordination). A one-way ANOSIM also demonstrates significant overall differences in distribution and significant pair-wise differences between all three calciphilic groups and the Ca-neutral group (Table 7). When limiting this analysis to the acidophilic species: *Danthonia decumbens*, *Deschampsia flexuosa*, *Gnaphalium sylvaticum*, *Rumex acetosella*, *Senecio sylvaticus*, *Vaccinium vitis-idaea* and *Veronica officinalis*; the moderately calciphilic species: *Filipendula vulgaris*, *Plantago lanceolata*, *Primula veris*, *Ranunculus polyanthemos* and *Tussilago farfara*; the strongly calciphilic

Table 4. Chemical properties of the soils of the investigated sites. Ranges are given in parentheses. n = the number of soil samples analyzed.

	pH	Ca (g l^{-1})	P (mg l^{-1})	K (mg l^{-1})	Mg (mg l^{-1})	NO_3 (mg l^{-1})
1. Bovik	6.91 ± 1.0	9.18 ± 18.46	2.3 ± 1.8	60.7 ± 38.5	217.4 ± 257.7	2.2 ± 1.7
n = 10	(4.9–8.0)	(0.5–60)	(0.1–5.1)	(9–138)	(52–925)	(1–4.2)
2. Markusböle	7.28 ± 0.89	10.77 ± 11.56	3.7 ± 4.5	55.6 ± 39	130.7 ± 119.6	1.65 ± 0.6
n = 10	(5.0–8.0)	(0.49–30.54)	(0.2–14.8)	(19–142)	(24.8–367)	(1–2.5)
3. Hulta	8.4 ± 0.2	41.3 ± 22.9	1.8 ± 0.9	90 ± 55.5	305.1 ± 191.6	1.15 ± 0.81
n = 15	(7.9–8.6)	(78.8–60)	(0.6–3.2)	(28.5–255)	(104–733)	(0.3–3.4)
4. Knutsboda	7.7 ± 1.0	22.4 ± 24.92	3.2 ± 1.6	39.8 ± 23.7	108.3 ± 112.1	1 ± 0
n = 12	(6.4–8.0)	(0.64–51.1)	(1.4–7.0)	(17.3–39.8)	(14–157)	(1–1)
5. Tengsöda	7.5 ± 1.0	32.80 ± 27.27	3.1 ± 3.0	63.8 ± 37.8	141.3 ± 78.2	1.62 ± 1.17
n = 14	(5.4–8.5)	(0.05–60)	(0–11)	(9–139)	(4–252)	(0.3–4.4)
6. Brännbolstad	6.0 ± 0.7	4.47 ± 4.43	3.2 ± 0.7	154.9 ± 58.3	229.7 ± 117.3	< 1
n = 13	(5.0–7.4)	(1.12–18.21)	(2–4)	(86–304)	(98–526)	(< 1–1.1)
7. Dånö	8.2 ± 0.4	34.9 ± 26.39	22.6 ± 19.1	119.6 ± 121.1	254 ± 105.5	3.73 ± 4.1
n = 14	(7.5–9.0)	(4.01–60)	(3–45)	(13–366)	(34–487)	(1–15)
8. Högbolstad	7.5 ± 1.1	22.41 ± 28.34	4.7 ± 2.8	72.4 ± 90.3	63.4 ± 89.7	1.34 ± 0.5
n = 7	(5.6–8.7)	(0.16–60)	(2–9)	(14–269)	(7–243)	(0.5–2.1)
9. Stålsby	8 ± 0.3	39.52 ± 21.89	6.8 ± 9.0	78.5 ± 42.2	146.5 ± 82.1	2.12 ± 2.01
n = 6	(7.7–8.3)	(2.23–60)	(2–25)	(45–154)	(20–258)	(0.6–5.7)

Table 5. Spearman correlations coefficients for the investigated variables (p values in parentheses). Species and calciphiles corrected refer to adjustments made in the numbers due to differences in the size of the investigated areas. Significant (p < 0.05) correlations are indicated with boldface.

	pH	Ca	P	K	Mg	NO_3	Area
Ca	**0.929**						
	(**0.003**)						
P	0.176	0.142					
	(0.650)	(0.715)					
K	0.192	0.267	0.201				
	(0.620)	(0.488)	(0.604)				
Mg	0.293	0.283	–0.243	0.700			
	(0.444)	(0.460)	(0.529)	(0.197)			
NO_3	0.134	0.209	0.395	0.276	0.422		
	(0.730)	(0.589)	(0.293)	(0.340)	(0.036)		
Area	–0.563	**–0.563**	–0.227	–0.059	–0.259	–0.445	
	(0.114)	(**0.032**)	(0.470)	(0.840)	(0.500)	(0.230)	
Species number	–0.494	–0.550	–0.243	–0.683	–0.317	0.293	0.544
	(0.177)	(0.125)	(0.529)	(0.064)	(0.406)	(0.444)	(0.130)
Calciphiles	0.410	–0.533	–0.343	0.222	–0.050	0.226	0.611
	(0.273)	(0.139)	(0.366)	(0.446)	(0.898)	(0.559)	(0.081)
Species corrected	0.636	**0.750**	0.243	0.233	0.200	0.460	**–0.979**
	(0.066)	(**0.020**)	(0.529)	(0.546)	(0.606)	(0.213)	(**0.000**)
Calciphiles corrected	0.661	**0.717**	0.059	0.217	0.500	0.577	**–0.862**
	(0.053)	(**0.030**)	(0.881)	(0.576)	(0.170)	(0.104)	(**0.003**)

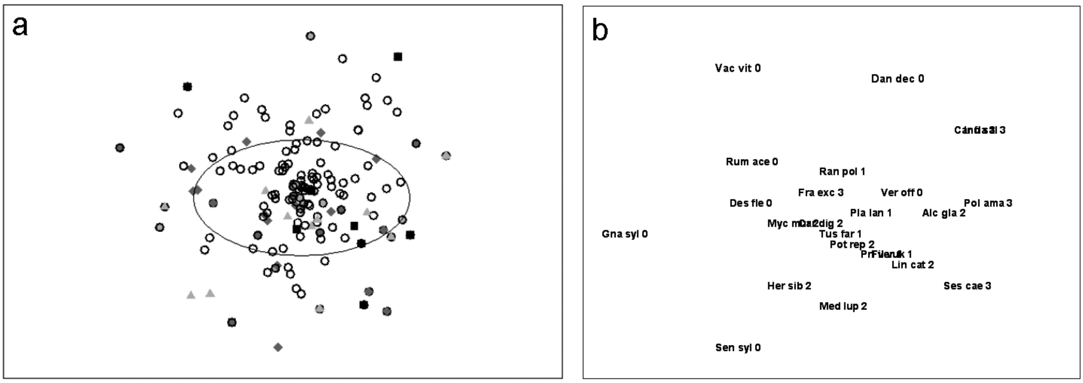

Fig. 5. NMDS ordinations based on species distribution patterns over sites: (**a**) species were grouped after Eklund (1946) into Ca-neutral (circles), moderately calciphilic (light-grey triangles), strongly calciphilic (dark-grey diamonds) and strictly Ca-dependent (black squares), the ellipse indicates where the selected subset of species analysed below clusters (note that the vast majority of the 414 species are overlapping in their distribution over sites and cannot therefore be made visible in the ordination), (**b**) a detailed analysis (data from within the ellipse in panel **a** only) using a number of specified, named species belonging to each of the four groups: 0 = acidophilic, 1 = moderately calciphilic, 2 = strongly calciphilic, 3 = Ca-dependent.

species: *Alchemilla glaucescens*, *Carex digitata*, *Heracleum sibiricum*, *Linum catharticum*, *Medicago lupulina*, *Mycelis muralis* and *Potentilla reptans* as well as the Ca-dependent species: *Carex flacca*, *Fraxinus excelsior*, *Inula salicina*, *Polygala amarella* and *Sesleria caerulea* some further clarifying patterns appear (Fig. 5b). First, notice the position of *Tussilago farfara*, the only species in this analysis that was present at all nine sites and thereby is located in the middle of the ordination scheme, as well as that there are three pairs of species, coincidentally belonging to the same group, which had exactly the same distribution over sites: the moderately calciphilic species *F. vulgaris* and *P. veris*, the strongly calciphilic species *C. digitata* and *M. muralis* as well as the Ca-dependent *C. flacca* and *I. salicina*. Second, the previous distribution with Ca-neutral (here: acidophilic) species placed in the upper part of the ordination scheme and the calciphilic species located in the lower part of Fig. 5a, persists in Fig. 5b and is now even refined with acidophilic species to the upper left and various levels of calciphilic species to the lower right. Third, the one-way ANOSIM on differences in the distribution of species over sites shows as before clearly significant differences between acidophilic and calciphilic species, but now also differences between the Ca-dependent species and the two other groups of calciphilic species (Table 7). Also a gradient from wet to dry habitat conditions is implied when going from the right to the left and from nutrient-rich to nutrient-poor conditions from the bottom to the top of the ordination scheme according to the description of respective plant in Mossberg *et al.* (1992).

Table 6. Results of BIO-ENV analysis listing the subsets of environmental variables that induces the best correlation between an environmental similarity matrix and a species/site similarity matrix.

Spearman correlation	Variable selections
All species	
0.394	P
0.389	P and pH
0.384	P and NO_3
0.364	P, Area and Mg
Calciphiles only	
0.344	P, Mg and NO_3
0.344	P and Mg
0.332	Mg
0.332	Mg and NO_3
0.331	Mg and pH

Discussion

None of the hundred most common plants in Finland (Botaniska museet 2007) is regarded as calciphilic; many of those are found at almost any chosen site on Åland. The value of 28.5% calciphiles among our plants also accords fairly well with other investigations. The decrease in calciphiles when going in an easterly direction over Åland is in accordance with Brenner (1930) and Eklund (1935), who claim that the calcium content of the soils is higher in the western parts. When the species lists of Jonsell and Jonsell (1981) from an area of NW Åland is analysed, one ends up with values of about 21%–22%; the proportion of calciphiles in NE Åland given by Valtonen (2003) is about 17%. This is still lower than might be expected, assuming that the calciphiles of Eklund (1946) will make up about one third of the total number of species (about 650) on the Åland Islands. On the other hand, some species lists of areas adjacent to the Lumparn Bay, with abundant Ordovician limestone (Hausen 1964), show that between 40%–70% of the plants are calciphiles (C.-A. Hæggström unpubl. data). We do not have any soil data from those areas. Although the registered calcium values in this study (24.19 g l^{-1}, range 0.05–60 g l^{-1}) vary much, they are still much higher than mean values for forest soils all over the Åland mainland (mean ± SD = 1.09 ± 3.97 g l^{-1}, range 0.01–43.50 g l^{-1}, N = 85), as recalculated from Högnäs (1966).

The five groups in the "all plants" NMDS analysis (Fig. 3a) may be due to the fact that the Markusböle and Bovik sites are still grazed by cattle and/or sheep and the Högbolstad site is isolated and surrounded by dense coniferous forest with low species diversity. The same partly applies to Hulta and Stålsby, which are surrounded by coniferous forests and cultivated fields, and to Brännbolstad, which was a wooded meadow between coniferous forest and the sea shore until some decades ago. The three sites: Dånö, Tengsöda and Knutsboda, have experienced various kind of disturbance due to grazing, gravel excavation and road construction. The NMDS based on calciphiles (Fig. 3b) gives a somewhat different picture, where Hulta and Brännbolstad become separate groups.

In the SAR-equations, the z values of 0.312 for all plants and 0.471 for calciphilic plants, respectively, seem a little bit high since the plots investigated are not true islands, and plants may disperse freely provided they are present in the local species-pool. However, the higher value for calciphiles may indicate a longer distance between "shell gravel islands" for those plants dependent on calcium. What further complicates the interpretation of the results, is that even though the deposits may be seen as islands, they are not truly isolated. Between the shell gravel deposits, the ground is locally rich in Ordovician limestone masking the effects of shell gravel. This will level out the differences in the calcium contents of the soils and make the landscape less patchy.

We found a positive correlation between number of plant species and calcium content but the highest proportions of calciphiles were not found on shell gravel. It thus appears that high concentrations of Ca are not inhibitory to plants, but that low Ca-levels are probably not sufficient for the calciphilic plants. This is in agreement

Table 7. One-way ANOSIM of differences in species distributions over sites between species grouped into four groups based on their dependency on Ca: 0 = neutral species, 1 = moderately calciphilic species, 2 = strongly calciphilic species, 3 = strictly calcium-dependent species. * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$, ns = not significant.

	All species		Selected widely-distributed species	
	R	*P*	*R*	*P*
Overall differences	0.117	0.001***	0.258	0.004**
Pair-wise differences				
0 *vs.* 1	0.112	0.003**	0.226	0.048*
0 *vs.* 2	0.125	0.001***	0.308	0.003**
0 *vs.* 3	0.121	0.046*	0.340	0.021*
1 *vs.* 2	–0.004	0.559 ns	–0.153	0.922 ns
1 *vs.* 3	–0.041	0.749 ns	0.514	0.008**
2 *vs.* 3	–0.036	0.749 ns	0.508	0.001***

with our main hypothesis. The high number of species in Markusböle, Bovik, Knutsboda and Brännbolstad may result from all these sites being former wooded meadows and that two of them are still being grazed. The traditional handling of the wooded meadows included several measures during the year (*see* e.g. Hæggström 1983), each of which could be regarded as a disturbance increasing the number of species by reducing competition. In fact, wooded meadows are among the most species-rich plant communities on the Åland Islands. Supposedly, the areas of Lumparn Bay, mentioned above, have calcium values of about 20 g l^{-1}, just like a cultivated field in that area (The Agri- and Horticultural Research Station of the Åland Islands unpubl. data).

The high occurrence of plants at high Ca-levels in turn makes us ask whether the calciphiles are, as often claimed, really dependent on Ca, or if they are just poor competitors at low Ca-levels but tolerate high Ca-levels. Different plant species may react differently to varying Ca-levels. Growth experiments could be carried out to elucidate this. Alternatively, instead of talking about calciphilic species one should use the word alkaliphilic, since high Ca-levels contribute to high pH. The very strong correlation between Ca and pH, both in the correlation analysis and in the PCA, implies that Ca indirectly affects plants via high pH and possibly the solubility of other macronutrients. Plants on calcaraeous soil may perhaps be dependent on higher concentrations of other nutrients (effect via the raised pH value). The close connection between Ca and pH could also partly explain the poor explanatory power of Ca alone in the BIO-ENV analysis. Calcium may, on the other hand, form water insoluble compounds, e.g. calcium phosphate, which hamper the uptake of phosphorus (e.g. Zohlen and Tyler 2004). So, perhaps the reason for a higher diversity at Ca-rich sites may be explained by the fact that plants growing there might be better competitors at low levels of phosphorus. This in turn raises further questions: Should we rather use the word alkaliphilic? Are plants Ca-dependent or Ca-tolerant? Could the whole story be about P and not Ca? The concentration of Ca in the cytoplasm of the plant cell is extremely low, while some organelles (i.e. dictyosomes, plastids and vacuols) may contain higher amounts of Ca. A re-run of BIO-ENV with pH excluded (due to the high correlation between pH and Ca with a Spearman correlation coefficient of 0.929) did not, however, lead to any changes for Ca, nor for the other remaining variables from the list of the most determinative environmental variables.

We cannot claim that any species found on shell gravel is restricted to that kind of substratum, with the possible exception for *Equisetum variegatum*. It is true that the oldest known locality of *E. variegatum* in the Åland Islands was a moist seashore meadow. It disappeared, however, from this place a few years ago. One other locality was a Ca-rich moist meadow. All the other findings of *E. variegatum*, one old and four recent, are in gravel pits. In the Åboland/Turku archipelago, five of the plants, i.e. *Allium ursinum*, *Ranunculus fallax* (included in the *R. auricomus* complex), *Potentilla reptans*, *Galium odoratum* and *Campanula rapunculoides*, were found only on shell gravel (Olsoni 1943). Of these, the species of the *R. auricomus* complex and *P. reptans* are common anywhere in meadowland on Åland and the other three are occasionally found in rich deciduous forests or meadows. Most of the plants mentioned by Olsoni (1943) are regarded as calciphiles by Eklund (1946), but there are also borderline cases, e.g. *Hepatica nobilis*, *Anemone nemorosa*, *Vicia sylvatica* and *Corylus avellana*. Of these four, *V. sylvatica* seems to be found also on rather acid nutrient-poor soils, while the others generally seem to grow in more basic and nutrient-rich habitats. The same applies to the plants mentioned by Halden (1920, 1921) in northern Sweden, where, e.g. *Satureja acinos*, *Satureja vulgaris*, *Daphne mezereum*, *Gagea lutea*, *Lonicera xylosteum*, *Paris quadrifolia*, *Primula veris* and *Viola mirabilis* were classified as calciphiles, while e.g. *Hepatica nobilis*, *Filipendula ulmaria*, *Viburnum opulus*, *Vicia sylvatica*, *Fragaria vesca*, *Polygonatum odoratum* and *Ribes alpinum* were regarded as southerly plants growing in places which are beneficial due to climatic or edaphic factors. Such places may be located on southern hill slopes for which the Swedes use the term *sydväxtberg* (= "hill of southerly plants"). Concerning the plants of Hallberg (1971), it is rather difficult to make any comparisons, since these species pools differ considerably from our material.

The exact meaning of the significantly different clustering of the calciphilic species from the Ca-neutral species in the "species-only" NMDS-ordination (Fig. 5) is hard to evaluate, but these results may give a hint that many calciphiles could be poor generalists and/or that the Ca concentration not always was sufficiently high at all shell-gravel sites. It also demonstrates the functionality of dividing species into these four groups with regard to Ca dependency, especially if the Ca-neutral group consists of solely acidophilic species. This finding may thus be seen as a support for a continuing use of calciphilic plants as indicators for rough assessments or initial screenings of plant diversity in applied conservation.

The occurrence of a certain plant at a certain place also depends on whether the plant occurs in the regional or the local species pool (Zobel 1997), and on whether the plant has a good or poor dispersal ability. The rather low similarity values between the different sites and the fact that only 18 plants (4.3% of the total species pool) were common to all sites may imply that the actual species composition of a single site is highly dependent on random factors. In the shell gravel sites one must also consider the possibility that the seed bank is activated when new pits are opened, although Wagner *et al*. (2003) found that most grasses and sedges of former meadows do not survive as seeds for a long time. None of our investigated sites is actually located in the middle of farming areas or close to pastures, except for Bovik and Markusböle, but instead rather close to forests. Also, in the cases where the shell gravel is close to areas affected by man and animals, the forest is very close to the shell gravel deposit in one direction or the other. It seems obvious, however, that the most species rich plots are areas that were used as wooded meadows or pastures quite recently or are otherwise affected by man and animals. The gravel deposits have not been available to plants until they have been uncovered in connection with road works, gravel excavation or ditching.

It seems that when discussing the distribution of plants, there are different reactions to calcium in different geographic areas (cf. Sterner 1922, Pedersen 1962, Hæggström 1986) and that also climatic factors should be taken into consideration. It is known from other taxa, e.g. snails, that low values of one environmental variable can be compensated by high values of another (Økland 1990). Since the BIO-ENV analysis did not rank calcium among the variables most important for the determination of the species composition, we rather suggest that the effects of calcium are indirect and partly show via high pH or that high calcium levels promote plant species that are poor competitors concering phosphorus. Many of the encountered calciphilic species do not occur or are rare on the Finnish mainland, and in Sweden they mainly occur in the "continental triangle" of eastern Sweden, from Gävle in the north to Scania (Skåne) in the south and including the limestone islands Öland and Gotland. We thus suggest that at least the strictly limestone-dependent and strongly-calciphilic species, but maybe also some moderately-calciphilic species, may be good indicators in Scandinavian conservation biology for identification of areas with potentially high biodiversity.

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Appendix. Species recorded at the study sites sites. Ca^{+} = moderately calciphilic, Ca^{++} = strongly calciphilic and Ca^{+++} = strictly limestone dependent. 0 = absent, 1 = present.

	Bovik	Markusböle	Stålsby	Dånö	Hulta	Högbolstad	Knutsboda	Tengsöda	Brännbolstad
Acer platanoides Ca^{+}	1	0	0	1	0	1	0	1	1
Achillea millefolium	1	1	1	1	1	1	1	1	1
Achillea ptarmica	0	1	0	1	1	0	0	1	0
Actaea spicata Ca^{++}	1	0	0	0	0	0	0	0	0
Aegopodium podagraria	0	1	1	1	1	0	0	1	1
Agrimonia eupatoria Ca^{+}	1	1	1	1	0	0	0	1	0
Agrostis capillaris	1	1	1	0	1	0	1	1	1
Agrostis gigantea	1	1	0	1	0	1	1	1	0
Agrostis stolonifera	1	1	0	0	1	0	0	0	1
Agrostis vinealis	1	0	0	0	0	0	1	0	0
Alchemilla filicaulis Ca^{+}	0	0	0	0	0	0	1	0	0
Alchemilla glaucescens Ca^{++}	1	1	0	0	1	0	1	0	1
Alchemilla monticola	1	1	0	0	1	0	1	1	0
Alchemilla samuelssonii Ca^{+++}	0	0	0	0	0	0	1	0	0
Alchemilla subcrenata	0	1	0	0	0	0	0	0	0
Alchemilla acutiloba	0	1	0	0	0	0	0	0	0
Alisma plantago-aquatica Ca^{+}	0	1	0	0	1	1	0	1	0
Allium oleraceum Ca^{+}	1	1	0	1	0	0	0	1	0
Allium schoenoprasum	1	0	0	0	0	0	0	0	0
Allium vineale Ca^{++}	0	0	0	0	0	0	0	1	0
Alnus glutinosa	1	1	0	1	0	1	1	1	1
Alopecurus geniculatus	0	1	0	0	0	1	0	1	0
Alopecurus pratensis	0	0	0	1	0	0	0	1	1
Anchusa officinalis	0	0	0	1	0	0	0	0	0
Anemone nemorosa	1	1	1	0	0	1	0	1	1
Anemone ranunculoides Ca^{+}	0	1	0	0	0	0	0	0	0
Angelica sylvestris	1	0	1	1	0	0	1	1	1
Antennaria dioica	0	1	0	0	0	0	0	0	0
Anthoxantum odoratum	1	1	0	1	0	0	0	0	0
Anthriscus sylvestris	1	1	0	1	1	1	1	1	1
Anthyllis vulneraria Ca^{++}	0	0	0	0	0	0	1	0	0
Arabidopsis thaliana	0	0	1	0	0	0	1	1	0
Arabis glabra	0	0	0	0	0	1	0	0	0
Arabis hirsuta Ca^{++}	1	1	0	0	0	0	1	1	0
Arctium minus	0	0	0	0	0	1	0	0	0
Arctium tomentosum	0	0	0	0	0	0	0	1	0
Arenaria serpyllifolia Ca^{++}	0	0	1	1	0	0	1	0	0
Artemisia vulgaris	0	0	0	1	0	0	1	1	0
Athyrium filix-femina	1	0	0	0	0	0	0	0	0
Atriplex patula	0	0	0	0	0	0	0	1	0
Avena sativa	0	0	0	0	0	0	0	1	0
Avenula pubescens	1	1	0	1	1	0	1	0	1
Barbarea stricta	1	0	0	0	0	0	0	0	0
Barbarea vulgaris	0	0	0	0	0	0	0	1	0
Betula pendula	1	1	1	1	1	1	1	1	1
Betula pubescens	1	1	0	0	0	1	1	1	0
Bidens tripartita	0	1	0	0	0	0	0	1	0
Bistorta vivipara Ca^{+}	0	1	0	0	0	0	0	0	0
Blysmus compressus Ca^{++}	0	1	0	0	0	0	0	0	0
Brachypodium sylvaticum Ca^{+++}	1	0	0	0	0	0	0	0	0

continued

Appendix. Continued.

	Bovik	Markusböle	Stålsby	Dånö	Hulta	Högbolstad	Knutsboda	Tengsöda	Brännbolstad
Brassica napus ssp. *oleifera*	0	0	0	0	0	1	0	0	0
Briza media Ca^{++}	1	1	0	0	1	0	0	1	1
Bolboschoenus maritima	0	1	0	0	0	0	0	0	0
Calamagrostis epigejos	1	1	0	0	1	1	1	1	1
Calamagrostis purpurea	0	0	0	0	0	1	0	0	0
Calamagrostis stricta	0	1	0	0	0	0	0	0	0
Calluna vulgaris	1	0	0	0	0	0	0	0	0
Calystegia sepium	0	0	0	0	0	0	1	1	0
Campanula glomerata Ca^{++}	0	0	0	0	0	0	0	1	0
Campanula patula	0	0	0	0	0	0	1	0	0
Campanula persicifolia	1	1	1	0	0	1	1	1	1
Campanula rapunculoides	0	0	1	0	0	0	0	0	0
Campanula rotundifolia	0	1	1	1	0	0	1	1	1
Campanula trachelium Ca^{++}	0	1	0	1	0	0	1	0	0
Capsella bursa-pastoris	0	1	0	1	0	1	0	1	0
Cardamine hirsuta Ca^{+}	0	0	0	0	0	0	1	0	0
Cardamine pratensis	1	1	0	1	0	0	0	0	0
Carex canescens	0	0	0	0	0	1	0	0	0
Carex caryophyllea Ca^{++}	0	1	0	0	0	0	0	0	0
Carex demissa Ca^{+}	0	0	0	0	1	0	0	0	0
Carex digitata Ca^{++}	1	1	1	1	0	1	1	1	1
Carex distans Ca^{+++}	1	0	0	0	0	0	0	0	0
Carex disticha Ca^{+}	1	0	0	0	1	0	0	0	0
Carex echinata	1	0	0	0	0	0	0	0	0
Carex elata Ca^{+}	1	0	0	0	0	0	0	0	0
Carex extensa Ca^{++}	1	0	0	0	0	0	0	0	0
Carex flacca Ca^{+++}	1	1	0	0	0	0	1	0	0
Carex flava Ca^{+++}	0	0	0	0	1	0	0	0	0
Carex hirta Ca^{+}	0	0	1	0	0	0	1	0	0
Carex muricata Ca^{+}	0	0	0	0	0	0	1	0	0
Carex nigra	1	1	0	0	1	0	0	0	0
Carex ovalis	0	0	0	0	0	1	1	0	1
Carex pallescens	1	1	0	1	1	1	1	1	0
Carex panicea Ca^{+}	1	1	0	0	1	0	0	0	0
Carex pilulifera	1	0	0	0	0	1	0	1	0
Carex pseudocyperus Ca^{++}	0	1	0	0	0	0	0	0	0
Carex pulicaris Ca^{+++}	1	0	0	0	0	0	0	0	0
Carex rostrata	1	1	0	0	0	1	0	0	0
Carex spicata	0	0	0	1	1	1	1	1	1
Carex vesicaria	1	0	0	0	0	0	0	0	0
Carex viridula	1	0	0	0	1	0	0	0	0
Carum carvi	0	1	1	0	0	0	0	0	0
Centaurea cyanus	0	1	0	0	0	0	0	1	0
Centaurea jacea	1	1	1	1	1	0	1	1	1
Cephalanthera longifolia Ca^{++}	1	0	0	0	0	0	0	0	0
Cerastium fontanum	1	0	0	1	0	1	1	1	1
Chelidonium majus	0	1	0	0	0	0	1	1	0
Chenopodium album	0	0	0	1	0	0	1	1	0
Cirsium arvense	1	1	1	1	1	1	1	1	1
Cirsium helenioides	0	1	0	0	0	0	0	0	0
Cirsium palustre	1	1	0	0	0	1	0	0	0

continued

Appendix. Continued.

	Bovik	Markusböle	Stålsby	Dånö	Hulta	Högbolstad	Knutsboda	Tengsöda	Brännbolstad
Cirsium vulgare	1	1	0	1	1	1	1	1	1
Comarum palustre	0	1	0	0	0	0	0	0	0
Convallaria majalis	1	1	0	1	0	0	0	0	0
Corydalis solida	1	1	0	0	0	0	0	0	1
Corylus avellana	0	1	0	1	0	0	1	0	1
Cotoneaster scandinavicus Ca^{+}	1	0	0	0	0	0	0	0	0
Crataegus rhipidophylla Ca^{++}	0	1	0	0	0	0	0	0	0
Cystopteris fragilis Ca^{++}	0	0	0	0	0	0	0	0	1
Dactylis glomerata	1	1	1	1	1	1	1	1	1
Dactylorhiza fuchsii Ca^{++}	1	0	0	0	0	0	0	0	0
Dactylorhiza maculata	0	0	0	0	0	1	0	0	0
Dactylorhiza sambucina Ca^{++}	1	1	0	0	0	0	0	0	0
Danthonia decumbens	1	1	0	0	0	0	0	1	0
Daphne mezereum Ca^{++}	1	0	0	0	0	0	0	0	0
Deschampsia cespitosa	1	1	1	0	1	1	1	1	1
Deschampsia flexuosa	1	0	1	0	0	1	1	1	1
Dianthus deltoides	0	1	0	0	0	0	0	0	0
Digitalis purpurea	0	0	0	0	0	1	0	0	0
Dryopteris carthusiana	1	0	0	0	0	0	0	0	0
Dryopteris filix-mas	1	1	0	0	0	0	0	0	1
Eleocharis palustris	0	1	0	0	1	1	0	0	0
Eleocharis uniglumis	1	0	0	0	0	0	0	0	0
Elymus caninus Ca^{+}	1	0	0	0	0	1	0	0	0
Elymus repens	0	1	1	1	1	1	1	1	0
Empetrum nigrum ssp. *hermaphroditum*	1	0	0	0	0	0	0	0	0
Empetrum nigrum ssp. *nigrum*	1	0	0	0	0	0	0	0	0
Epilobium adenocaulon	0	0	0	1	0	1	1	1	0
Epilobium angustifolium	0	0	1	1	0	1	1	1	0
Epilobium ciliatum	0	0	0	1	0	1	0	1	0
Epilobium collinum Ca^{++}	0	0	1	0	0	0	0	0	0
Epilobium montanum Ca^{+}	1	0	0	1	0	0	1	1	0
Epilobium palustre	0	1	0	0	0	0	0	0	0
Epilobium parviflorum Ca^{++}	0	0	0	1	0	1	1	0	1
Equisetum arvense	1	1	1	1	1	1	1	1	0
Equisetum hyemale Ca^{+}	0	0	0	0	0	1	0	0	0
Equisetum palustre Ca^{++}	0	0	0	0	0	0	1	0	0
Equisetum pratense Ca^{+}	0	0	0	0	0	1	0	0	0
Equisetum variegatum Ca^{+++}	0	0	0	0	0	0	1	0	0
Erigeron acer Ca^{++}	0	0	0	1	0	0	1	0	0
Eriophorum angustifolium	1	0	0	0	0	0	0	0	0
Erophila verna Ca^{+}	0	1	0	0	0	0	0	0	0
Erysimum cheirantoides	0	0	0	1	0	0	0	1	0
Euphrasia cf. *nemorosum*	0	1	0	0	0	0	0	0	0
Euphrasia stricta	1	1	0	0	0	0	0	1	0
Fallopia convolvulus	0	0	0	0	0	0	0	1	0
Festuca elatior	1	1	0	1	0	1	1	0	1
Festuca pratensis	0	0	0	1	1	0	0	1	1
Festuca ovina	1	1	1	1	0	1	0	1	1
Festuca rubra	1	1	1	1	1	1	1	1	1
Filago arvensis	0	0	0	1	0	0	0	0	0
Filpendula ulmaria	0	1	1	1	1	0	1	1	1

continued

Appendix. Continued.

	Bovik	Markusböle	Stålsby	Dånö	Hulta	Högbolstad	Knutsboda	Tengsöda	Brännbolstad
Filipendula vulgaris Ca^{+}	1	1	0	1	1	0	1	1	1
Fragaria vesca	1	1	1	1	1	1	1	1	1
Fraxinus excelsior Ca^{+++}	1	1	0	0	0	1	1	1	1
Fumaria officinalis	0	0	0	1	0	0	0	1	0
Gagea lutea Ca^{+}	0	0	0	0	0	0	0	0	1
Galeopsis bifida	0	0	0	0	0	0	0	1	0
Galeopsis speciosa	0	0	0	0	0	0	0	1	0
Galeopsis tetrahit	0	0	0	0	0	1	0	0	0
Galium album	0	0	0	0	0	0	1	1	0
Galium album × *verum*	0	0	0	0	0	0	1	0	0
Galium aparine Ca^{+}	0	0	0	1	0	0	0	0	0
Galium boreale	1	1	1	1	1	1	1	1	1
Galium palustre	1	1	0	1	1	1	1	0	1
Galium spurium	0	0	0	0	0	1	0	0	0
Galium uliginosum	0	0	0	0	1	1	0	0	0
Galium verum	1	1	1	1	1	1	1	1	1
Gentianella amarella Ca^{++}	0	1	0	0	0	0	0	0	0
Geranium pusillum	1	0	0	1	0	0	0	0	0
Geranium robertianum Ca^{++}	1	0	0	0	0	0	0	0	0
Geranium sanguineum Ca^{+}	1	0	0	0	0	0	1	1	0
Geranium sylvaticum	1	1	0	0	1	0	1	1	1
Geum rivale	1	1	0	0	1	0	1	0	1
Geum urbanum Ca^{+}	1	1	0	1	0	0	0	1	0
Glaux maritima	1	1	0	0	0	0	0	0	0
Glechoma hederacea	1	1	0	0	0	0	0	0	0
Gnaphalium sylvaticum	0	0	0	0	0	1	0	1	1
Gnaphalium uliginosum	0	0	0	0	0	1	0	1	0
Glaux maritima	1	1	0	0	0	0	0	0	0
Glyceria fluitans	0	0	0	0	0	1	0	0	0
Gymnocarpium dryopteris	0	0	0	0	0	1	0	0	0
Helianthemum nummularium Ca^{++}	0	1	0	0	1	0	1	0	0
Hepatica nobilis	1	1	1	1	0	0	0	1	1
Heracleum sibiricum Ca^{++}	1	0	0	1	0	0	1	1	1
Hieracium sylvatica	0	0	1	0	0	0	0	0	0
Hieracium umbellatum	1	0	0	0	1	0	1	1	0
Hieracium gr. *Vulgata*	0	0	1	1	0	0	0	0	0
Hippophaë rhamnoides Ca^{+++}	1	0	0	0	1	0	0	0	0
Hylotelephium maximum	1	0	0	1	0	0	0	0	0
Hypericum maculatum	1	1	0	1	1	1	1	1	1
Hypericum perforatum	1	0	1	1	0	0	1	0	0
Impatiens glandulifera	0	0	0	0	0	0	0	1	0
Inula salicina Ca^{+++}	1	1	0	0	0	0	1	0	0
Juncus articulatus	1	0	0	1	1	1	1	1	0
Juncus bufonius	0	0	0	0	0	1	0	0	0
Juncus compressus	0	1	0	0	0	0	0	0	0
Juncus conglomeratus	1	0	0	1	0	1	1	1	0
Juncus effusus	0	1	0	1	0	1	1	1	1
Juncus filiformis	0	0	0	0	0	1	0	0	0
Juncus gerardii	1	1	0	0	0	0	0	0	0
Juniperus communis	1	1	0	1	1	0	1	1	1
Knautia arvensis	0	0	0	0	0	0	1	0	0

continued

Appendix. Continued.

	Bovik	Markusböle	Stålsby	Dånö	Hulta	Högbolstad	Knutsboda	Tengsöda	Brännbolstad
Lamium album	0	0	0	0	0	1	0	0	0
Lapsana communis	1	0	0	1	0	1	1	1	0
Laserpitium latifolium Ca++	0	0	0	0	0	0	1	0	0
Lathyrus pratensis	1	1	1	1	1	0	1	1	1
Lathyrus vernus	1	0	0	0	0	0	0	0	0
Ledum palustre	1	0	0	0	0	0	0	0	0
Leontodon autumnalis	1	1	0	0	1	1	1	1	0
Leucanthemum vulgare	0	1	1	1	1	0	1	1	1
Linum catharticum Ca++	1	1	0	1	1	0	1	1	0
Listera ovata Ca+	1	1	0	0	0	1	1	1	0
Lolium perenne	0	0	0	0	0	0	0	1	0
Lonicera xylosteum Ca++	1	0	0	1	0	0	0	0	1
Lotus corniculatus	0	0	1	0	1	0	0	1	1
Luzula campestris	1	1	0	0	0	0	0	0	1
Luzula multiflora	1	1	0	0	1	1	1	1	0
Luzula pallidula	0	0	0	0	0	0	1	0	0
Luzula pilosa	1	1	1	0	0	1	1	1	1
Lychnis flos-cuculi	0	0	0	1	0	0	0	0	0
Lychnis viscaria	1	0	0	1	0	0	0	0	0
Lycopodium annotinum	1	0	0	0	0	0	0	0	0
Lycopus europaeus	0	1	0	0	0	0	0	0	0
Lysimachia thyrsiflora	0	1	0	0	0	1	1	1	0
Lysimachia vulgaris	1	1	0	1	0	0	1	1	1
Lythrum salicaria	1	1	0	0	0	0	0	0	0
Maianthemum bifolium	1	1	0	0	0	1	0	1	1
Malva moschata	0	0	0	1	0	0	0	0	0
Malus domestica × *sylvestris*	0	0	1	0	0	0	0	0	0
Malus sylvestris Ca+	1	1	0	0	0	0	0	0	0
Matricaria matricaroides	0	0	0	1	0	1	0	1	0
Medicago lupulina Ca++	1	0	1	1	1	0	1	1	0
Melampyrum nemorosum	1	0	0	0	0	0	1	0	0
Melampyrum pratense	1	0	0	1	0	1	0	0	1
Melampyrum sylvaticum	1	0	0	0	0	1	0	0	1
Melica nutans	1	1	0	1	1	1	1	1	1
Mentha aquatica	1	0	0	0	0	0	0	0	0
Mentha arvensis	0	1	0	0	0	0	1	0	0
Mentha × *verticillata*	0	1	0	0	0	0	0	0	0
Menyanthes trifoliata	1	0	0	0	0	0	0	0	0
Milium effusum Ca+	1	0	0	0	0	0	0	0	0
Moehringia trinervia	1	1	1	0	0	1	0	1	0
Molinia caerulea	1	1	0	0	0	0	0	0	0
Mycelis muralis Ca++	1	1	1	1	0	1	1	1	1
Myosotis arvensis	1	0	0	1	0	1	1	1	0
Myosotis laxa ssp. *caespitosa*	0	1	0	1	0	0	0	0	0
Myosotis stricta Ca+	0	0	0	0	0	0	0	1	0
Nardus stricta	1	1	0	0	0	0	0	0	0
Odontites vulgaris	0	1	0	0	0	0	0	0	0
Oxalis acetosella	0	1	1	0	0	1	0	0	1
Origanum vulgare Ca+	1	0	0	0	0	0	0	0	0
Orthilia secunda	0	0	1	0	0	1	0	1	0
Paris quadrifolia Ca+	1	1	1	0	0	0	0	0	1

continued

Appendix. Continued.

	Bovik	Markusböle	Stålsby	Dånö	Hulta	Högbolstad	Knutsboda	Tengsöda	Brännbolstad
Persicaria lapathifolia	0	0	0	1	0	0	0	1	0
Persicaria minor	0	1	0	0	0	0	0	0	0
Phalaris arundinacea	0	0	1	0	0	0	0	0	0
Phleum pratense	0	1	1	1	1	1	1	1	0
Phragmites australis	1	1	0	1	0	1	1	0	0
Picea abies	1	1	0	1	1	1	1	1	1
Pilosella cymosa s. lat.	1	0	0	1	0	0	1	1	0
Pilosella officinarum	1	1	0	0	0	0	1	1	0
Pilosella sp.	0	0	0	0	0	1	0	0	0
Pimpinella saxifraga	1	1	1	1	1	0	0	1	1
Pinus sylvestris	1	1	1	1	1	1	1	1	1
Plantago lanceolata Ca^{+}	1	1	1	0	1	0	1	1	1
Plantago major	1	1	1	1	0	1	1	1	1
Plantago maritima	1	0	0	0	0	0	0	0	0
Plantago media Ca^{++}	0	1	0	0	0	0	0	0	1
Platanthera bifolia	1	0	0	0	0	0	0	1	1
Platanthera chloranta Ca^{+}	0	0	0	1	0	0	0	0	0
Poa angustifolia	1	1	0	1	1	0	1	1	1
Poa annua	1	1	0	0	0	1	0	1	0
Poa compressa Ca^{++}	0	0	1	1	0	0	0	1	0
Poa nemoralis	1	0	1	1	0	0	1	1	1
Poa palustris	0	0	0	0	0	1	0	0	0
Poa pratensis	0	1	0	0	1	1	1	0	1
Poa subcaerulea Ca^{+}	0	1	0	0	0	0	0	0	0
Poa trivialis	1	0	0	1	0	1	1	1	1
Polygala amarella Ca^{+++}	1	1	0	0	1	0	1	0	0
Polygala vulgaris Ca^{+}	1	1	0	0	1	0	0	0	0
Polygonatum multiflorum Ca^{+}	0	1	0	0	0	0	0	0	0
Polygonatum odoratum	1	0	0	0	0	0	0	0	0
Polygonum aviculare	0	1	0	1	0	1	0	1	0
Polygonum minus	0	1	0	0	0	0	0	0	0
Polypodium vulgare	1	0	0	0	0	0	0	0	1
Populus tremula	1	1	0	0	0	0	1	1	1
Potentilla anserina	1	1	0	0	0	0	0	1	1
Potentilla argentea	1	0	0	0	0	0	1	1	0
Potentilla crantzii Ca^{++}	0	1	0	0	0	0	0	0	0
Potentilla erecta	1	1	0	0	1	0	1	1	1
Potentilla palustris	0	1	0	0	0	1	0	0	0
Potentilla reptans Ca^{++}	1	1	1	1	1	0	1	1	1
Primula farinosa Ca^{+++}	1	1	0	0	0	0	0	0	0
Primula veris Ca^{+}	1	1	0	1	1	0	1	1	1
Prunella vulgaris	1	1	0	0	1	1	1	1	1
Prunus padus	1	1	0	0	0	0	0	0	0
Pteridium aquilinum ssp. *pinetorum*	0	1	1	1	1	1	1	1	1
Pyrola minor	0	0	1	0	0	0	0	1	0
Quercus robur	1	0	0	0	0	0	0	0	0
Ranunculus acris	1	1	1	1	1	1	1	1	1
Ranunculus aquatlis	1	0	0	0	0	0	0	0	0
Ranunculus auricomus coll.	1	1	0	0	0	0	0	0	0
Ranunculus bulbosus Ca^{+}	1	0	0	0	0	0	0	0	0
Ranunculus flammula	1	1	0	0	0	1	1	0	1

continued

Appendix. Continued.

	Bovik	Markusböle	Stålsby	Dånö	Hulta	Högbolstad	Knutsboda	Tengsöda	Brännbolstad
Ranunculus peltatus ssp. *baudotii*	1	0	0	0	0	0	0	0	0
Ranunculus polyanthemos Ca+	1	1	1	0	0	0	1	1	1
Ranunculus repens	1	1	0	1	1	1	1	1	1
Ranunculus sceleratus	0	1	0	0	0	0	0	0	0
Rhamnus cathartica Ca++	1	1	0	0	0	0	0	0	0
Rhamnus frangula	1	0	0	0	1	0	0	1	0
Ribes alpinum	1	1	1	1	0	1	1	1	1
Ribes uva-crispa	0	0	0	0	0	0	0	1	0
Rorippa palustris	0	1	0	0	0	0	0	0	0
Rorippa sylvestris	0	0	0	1	0	0	0	0	0
Rosa dumalis ssp. *coriifolia*	1	1	1	1	1	0	1	1	1
Rosa dumalis ssp. *dumalis*	1	1	1	1	1	0	1	1	1
Rosa majalis	1	0	0	0	0	0	0	0	0
Rosa mollis Ca+	0	1	0	0	0	0	0	0	0
Rosa sherardii Ca++	0	1	0	0	0	0	0	0	0
Rubus idaeus	1	1	1	1	1	1	1	1	1
Rubus caesius Ca+++	1	1	0	0	0	0	0	0	0
Rubus saxatilis	1	1	1	0	1	0	1	1	1
Rumex acetosa	1	1	1	0	1	0	1	1	0
Rumex acetosella	1	0	1	0	0	1	1	1	0
Rumex crispus	0	1	0	0	0	0	1	1	1
Rumex longifolius	0	0	1	1	0	1	1	1	1
Sagina nodosa Ca++	0	0	0	0	0	0	1	0	0
Sagina procumbens	1	0	0	0	0	1	0	0	0
Salix aurita	1	0	0	0	0	1	1	0	0
Salix caprea	1	1	1	1	1	1	1	1	1
Salix cinerea	1	1	0	0	1	1	1	1	0
Salix cinerea × *myrsinifolia*	0	1	0	0	0	0	0	0	0
Salix myrsinifolia	0	1	0	0	0	0	1	0	0
Salix pentandra	0	1	0	0	1	1	1	1	0
Salix phylicifolia	1	1	0	0	1	1	1	1	0
Salix repens	1	0	0	0	0	0	0	1	0
Salix starkeana	1	1	0	0	0	1	1	1	0
Samolus valerandi Ca++	1	0	0	0	0	0	0	0	0
Sanicula europaea Ca++	1	1	0	0	0	0	0	0	1
Satureja acinos Ca+++	0	0	0	1	0	0	0	0	0
Satureja vulgaris Ca+	1	1	1	0	0	0	0	1	1
Saxifraga granulata Ca+	1	0	0	0	0	0	0	0	0
Scrophularia nodosa	1	0	0	1	0	1	0	0	1
Scutellaria galericulata	0	1	0	0	0	0	1	0	0
Secale cereale	0	0	0	0	0	1	0	0	0
Sedum acre Ca++	1	0	0	0	0	0	1	0	0
Sedum album Ca++	1	0	0	0	0	0	1	0	0
Selinum carvifolia	1	0	0	0	0	0	0	0	0
Senecio sylvaticus	0	0	0	1	0	1	1	1	0
Senecio viscosus	0	0	0	1	0	0	1	1	0
Sesleria caerulea Ca+++	0	1	0	0	1	0	1	1	0
Silene dioica	1	0	0	0	0	0	0	1	0
Silene latifolia ssp. *alba*	0	0	0	1	0	0	0	0	0
Silene nutans Ca+	1	0	0	0	0	0	1	0	0
Sinapis arvensis Ca++	0	0	0	1	0	0	0	0	0

continued

Appendix. Continued.

	Bovik	Markusböle	Stålsby	Dånö	Hulta	Högbolstad	Knutsboda	Tengsöda	Brännbolstad
Solanum dulcamara Ca+	0	1	0	0	0	0	0	0	0
Solidago virgaurea	0	1	0	0	0	0	0	0	1
Sonchus arvensis	0	0	0	0	1	0	0	0	1
Sonchus asper	0	0	0	1	0	0	1	1	0
Sorbus aucuparia	1	1	1	1	1	1	1	1	1
Sorbus hybrida	1	1	1	0	1	0	0	1	1
Sparganium sp.	0	0	0	1	0	0	0	0	0
Spergula arvensis	0	0	0	0	0	0	0	1	0
Stachys sylvatica Ca++	1	1	0	0	0	0	0	0	1
Stellaria graminea	1	1	0	1	1	0	1	1	1
Stellaria media	0	0	0	1	0	1	0	1	0
Tanacetum vulgare	1	1	1	0	0	0	0	1	0
Taraxacum balticum	1	0	0	0	0	0	0	0	0
Taraxacum sp.	1	1	1	1	1	1	1	1	1
Taxus baccata Ca++	0	0	0	1	0	0	0	0	0
Thalictrum flavum Ca+	0	1	0	0	0	0	0	0	0
Thlaspi arvensis	0	0	0	1	0	0	0	1	0
Thlaspi caerulescens	0	0	0	0	0	0	1	0	0
Torilis japonica Ca++	0	0	0	1	0	0	0	0	0
Tragopogon pratensis	0	0	0	0	0	0	1	0	0
Trientalis europaea	1	0	0	0	0	0	0	1	0
Trifolium fragiferum Ca++	0	1	0	0	0	0	0	0	0
Trifolium hybridum	0	0	0	0	0	0	0	1	0
Trifolium medium	1	1	1	1	1	0	1	1	1
Trifolium pratense	1	1	1	1	1	1	1	1	1
Trifolium repens	1	1	1	1	1	1	1	1	1
Triglochin maritima	1	0	0	0	0	0	0	0	0
Triglochin palustre	1	0	0	0	0	0	0	0	0
Tripleurospermum inodorum	1	1	0	0	0	1	1	1	0
Triticum aestivum	0	0	0	0	0	0	0	1	0
Tussilago farfara Ca+	1	1	1	1	1	1	1	1	1
Typha angustifolia Ca+	0	1	0	0	0	0	0	0	0
Typha latifolia	1	1	0	0	1	1	1	0	0
Ulmus glabra Ca+	0	0	0	1	0	0	0	0	0
Urtica dioica	1	1	1	1	0	1	1	1	1
Vaccinium myrtillus	1	1	1	1	0	1	0	0	1
Vaccinium vitis-idaea	1	0	1	0	0	0	0	1	0
Vaccinium uliginosum	1	0	0	0	0	0	0	0	0
Valeriana officinalis	1	1	0	0	0	0	1	1	0
Verbascum thapsus	1	1	1	1	0	0	1	1	1
Veronica arvensis	0	0	0	1	0	0	0	0	0
Veronica beccabunga Ca+++	0	0	0	1	0	0	0	0	0
Veronica chamaedrys	1	1	1	0	1	1	0	1	1
Veronica officinalis	1	1	0	0	1	1	1	1	0
Veronica scutellata	1	1	0	1	0	1	1	0	0
Veronica serpyllifolia	1	0	0	0	0	1	0	0	0
Veronica spicata Ca++	1	0	0	0	0	0	0	0	0
Viburnum opulus	1	1	0	1	0	0	0	0	1
Vicia cracca	1	1	1	1	1	1	1	1	1
Vicia hirsuta Ca++	0	0	0	1	0	0	1	1	0
Vicia sepium	1	1	1	0	0	0	1	1	0

continued

Appendix. Continued.

	Bovik	Markusböle	Stålsby	Dånö	Hulta	Högbolstad	Knutsboda	Tengsöda	Brännbolstad
Vicia sylvatica	1	0	0	0	0	1	0	0	1
Vicia tetrasperma Ca^{+}	0	0	1	0	0	0	0	1	0
Viola arvensis	1	0	0	1	0	0	1	1	0
Viola canina	1	1	0	0	0	0	1	0	0
Viola mirabilis Ca^{++}	1	0	0	0	0	0	0	0	1
Viola riviniana	1	1	1	0	0	0	1	1	1
Woodsia ilvensis Ca^{++}	1	0	0	0	0	0	0	0	0
Total	232	208	85	138	94	128	166	185	120