

The basiphilous dry grasslands of shallow, skeletal soils (Alysso-Sedetalia) on the island of Öland (Sweden), in the context of North and Central Europe

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with 6 figures and 5 tables

Abstract. We analysed the Northern European dry grassland communities of shallow, skeletal soils over base-rich bedrock (order Alysso-Sedetalia, subclass Sedo-Scleranthenea, class Koelerio-Corynephoretea) and compared them with their Central European counterparts. The study was based on our personal relevés from the southern part of the Baltic island of Öland (Sweden, $n = 182$) and on relevés from other Northern European regions ($n = 65$) and Central Europe ($n = 127$) compiled from the literature. Both cluster analyses and ordinations show a sharp floristic distinction between the Nordic and the Central European communities. We thus propose to establish a separate Nordic alliance *Tortello tortuosae-Sedion albi* alongside the temperate Alysso-Sedion. The Nordic communities are characterised by a number of taxa that are either endemic or occur widely disjunct from their main distribution ranges. In addition, the cryptogam layer of the *Tortello-Sedion* communities is generally much better developed than that of the Alysso-Sedion, in terms of both coverage and species richness. Within the *Tortello-Sedion*, we distinguish two suballiances with a total of six floristically well-defined associations, most of which are newly described: (1) *Tortello tortuosae-Sedenion albi* as a negatively differentiated suballiance of non-alvar stands, mostly from the Scandinavian mainland (*Cladonio symphycaepae-Sedetum albi*, *Ditricho flexicaulis-Sedetum acris*), and (2) *Tortello rigentis-Helianthemion oelandici* comprising the stands of the Nordic alvar areas (*Crepido pumilae-Allietum alvarensis*, *Fulgensio bracteatae-Poetum alpinae*, *Helianthemion oelandici-Galietum oelandici*, *Gypsophilo fastigiatae-Globularietum vulgaris*). “Alvars”, i.e. almost level areas with superficial Ordovician or Silurian limestone that are only sparsely covered by vegetation, are largely restricted to the Baltic islands of Sweden (Öland, Gotland) and to Estonia, and reach their greatest extent in southern Öland. The classification of the four Ölandic communities of the *Tortello-Helianthemion* is supported by an indirect ordination analysis whose axes clearly represent a gradient in environmental conditions. Soil depth and soil moisture are the most important differentiating factors. The *Crepido-Allietum* and the *Fulgensio-Poetum* grow at sites regularly inundated in winter. Whereas the first can be found on slightly deeper soils that are thus heavily affected by frost movement, the second inhabits the most shallow soils of all the communities and also shows the highest coverage of bare rock. The *Helianthemion-Galietum* and the *Gypsophilo-Globularietum* grow on more stable, less flooded and slightly deeper soils. The Nordic communities are characterised by extremely high species densities of vascular plants, bryophytes and lichens. With mean total values of 36.0–53.6 species on 4 m², they exceed their Central European counterparts two- to threefold. With up to 80 species on 4 m², the *Gypsophilo-Globularietum* is

one of the communities with the highest small-scale species richness documented so far. We discuss how the extraordinary phytodiversity of the Tortello-Sedion communities could have emerged. A large species pool due to a long-standing habitat continuity, high spatio-temporal small-scale heterogeneity, reduced competition, and the small size of the individual plants are probable causes.

Keywords: alvar vegetation, classification, species richness, syntaxonomy, Sedo-Scleranthenea, Tortello tortuosae-Sedion albi.

1 Introduction

The subclass Sedo-Scleranthenea of the Koelerio-Corynephoretea comprises dry grasslands of shallow skeletal soils that are especially rich in therophytic vascular plants, succulents, bryophytes and lichens (DENGLER et al. 2003). They can occur over compact bedrock and gravel but also on anthropogenic substrata (concrete slabs, wall tops), either acidic or base-rich. These vegetation types have two main distribution areas in Europe, the mountain ranges of temperate Europe on the one hand and the southern part of Northern Europe on the other (DENGLER 2003). In Central Europe, such dry grasslands, sometimes also misleadingly named “rock and outcrop communities”, have been well known for a long time and several synthesising studies are available (e.g. BRAUN-BLANQUET 1955, 1961, MÜLLER 1961, MORAVEC 1967, KORNECK 1975).

From Northern Europe, only basiphilous dry grasslands of shallow skeletal soils (Alysso-Sedetalia) have been described so far. Compared with their southern counterparts, they have a number of peculiarities: They can cover huge areas, especially in the “alvars” of Öland, Gotland (Sweden) and Saaremaa (Estonia), i.e. almost level Ordovician or Silurian limestone plateaus with a thin soil cover and a sparse vegetation, whereas in Central Europe these communities normally occupy only small patches between other dry grassland communities. The site conditions of the Nordic Alysso-Sedetalia stands are rather unusual for dry grasslands, as many of them face not only severe drought in summer but also inundation and frost movement in winter (e.g. ALBERTSON 1950, HALLBERG 1971). Bryophytes and lichens generally assume a much greater importance than in temperate Alysso-Sedetalia communities, both in terms of species richness and coverage (HALLBERG 1971). The species composition of Nordic dry grassland communities of shallow, skeletal soils deviates in many respects from their southern counterparts, and includes some endemics, species with a widely disjunct distribution and arctic-alpine taxa (e.g. ALBERTSON 1946, BENGTTSSON et al. 1988). They also show remarkably high overall species densities on small spatial scales (e.g. KRAHULEC et al. 1986).

On the Great Alvar, a large limestone plateau in the southern part of the Swedish island of Öland, Alysso-Sedetalia communities probably reach both their greatest extent and their highest diversity within the Nordic countries. ALBERTSON (1950) was the first to give a comprehensive but still rough description of the dry grasslands of the Great Alvar. He differentiated three major types, the “Sedetum”, the “Festucetum” and the “Ave-

netum". Apart from two short notes by Central European vegetation scientists, who tried to "attach" the alvar dry grasslands to supraregional phytosociological units on the basis of very few relevés (BRAUN-BLANQUET 1963, WESTHOFF et al. 1983), the system of ALBERTSON (1950), based on the Uppsala school of vegetation science, remained accepted widely and unchallenged for more than three decades. In 1986, KRAHULEC et al. proposed a new classification into four associations, based on a numerical analysis of 69 relevés, three of which belong to the dry grasslands of shallow, skeletal soils. The authors put forward suggestions regarding the position of the associations within the synsystematic system of the Braun-Blanquet approach, but they did not publish their syntaxa validly since they regarded their results as preliminary.

In Northern Europe outside the Great Alvar of Öland, similar vegetation types have been described from Gotland (e.g. DU RIETZ 1925, PETTERSON 1958, WESTHOFF et al. 1986), the Swedish mainland (e.g. ALBERTSON 1946, TÜXEN 1951, HALLBERG 1971), southern Norway (e.g. MARKER 1969, HALVORSEN 1980) and Estonia (e.g. PÄRTEL et al. 1999). However, a synthesising study comparing the units from the Great Alvar with those from other Nordic and Central European areas is still needed. For most of the Nordic communities, no valid syntaxon names are available and the meaning of the applied invalid or vernacular names may vary considerably between different sources. As a result of these unclear classifications and names, the distribution of the Nordic *Alysso-Sedetalia* communities is also only vaguely known.

Our paper is based mainly on a study of the dry grassland vegetation in southern Öland by LÖBEL (2002), which also included the *Koelerio-Corynepforenea* and the *Festuco-Brometea* in addition to the *Sedo-Scleranthenea*. The two first syntaxa will be the subject of separate publications. Aspects of the phytodiversity of all the Ölandic dry grassland communities were dealt with in LÖBEL et al. (2002, 2004, 2006). In this paper, we shall address the following questions concerning the dry grassland communities of shallow, skeletal soils (*Sedo-Scleranthenea*) in general, and their basiphytic order *Alysso-Sedetalia* in particular:

- What community types can be distinguished in Northern Europe and what environmental factors cause this variation?
- What are the differences between Nordic and Central European communities? What are the reasons and the taxonomic implications of these?
- How species rich are the Nordic communities compared to their Central European counterparts and to other vegetation types? What are the possible reasons for these phytodiversity patterns?

2 Study area

2.1 Northern Europe

We use the terms "Northern Europe" and "Nordic countries" for Norway, Sweden, Finland, the Russian part of the Baltic Shield and Estonia. The

latter country is included since it has close geological, phytogeographical and climatic relationships with Scandinavia proper, especially with the Swedish islands of Öland and Gotland.

The Nordic countries generally are characterised by Precambrian crystalline bedrocks of the Baltic Shield that are rather acidic and resistant to weathering (e.g. SJÖRS 1999). However, Cambrian and Ordovician sediments, which are often calcareous, locally cover the Precambrian stratum (e.g. EMBLETON 1984). Such sites are usually referred to as "alvar" in the ecological literature, a Swedish vernacular word, meaning an almost flat, unwooded area with superficial and often exposed limestone bedrock (ALBERTSON 1946, ZOBEL & KONT 1992). Where this bedrock has only a very thin soil cover of a few centimetres, communities of the *Alyso-Sedetalia* may occur. Such vegetation types are restricted to a few isolated localities in the southern part of Northern Europe. In Sweden, these are the islands of Öland and Gotland as well as some smaller areas in Öster- and Västergötland (e.g. ALBERTSON 1946). In Estonia, the islands of Saaremaa, Hiiumaa and Muhu (e.g. PÄRTEL et al. 1999) are the most important limestone districts. Small alvar areas also occur in Ahvenamaa in Finland and in the St. Petersburg district in Russia (PÄRTEL et al. 1999); however, no literature reports from these localities were available. In southern Norway, especially in the Oslo region, the bedrock is more diverse, consisting among others of Permian sediments partly rich in lime (e.g. MARKER 1969). In addition, HALLBERG (1971) and HALVORSEN (1980) have reported *Alyso-Sedetalia* communities as growing on acid rocks, gravel deposits or even sandy soils close to the beach line, where shell deposits or bird dung have increased the soil reaction secondarily.

The climate of the southern parts of Northern Europe shows a long gradient from mild winter temperatures and a high mean annual precipitation in southern Norway and on the Swedish west coast, to relatively continental conditions with low precipitation values on Öland, Gotland and in western Estonia. Throughout the whole region, the mean annual temperatures vary between 4–8 °C, the mean annual temperature amplitudes from 15–32 K, and the mean annual precipitation values from 450–2 800 mm (worldclim_10m; cf. NEW et al. 2002).

2.2 Öland and its Great Alvar

The greatest extent of shallow calcareous soils in Northern Europe is to be found on Öland. The superficial bedrock of the island consists of Cambrian and Ordovician sediments whose borderline is indicated by a ridge 15 to 20 metres in height in the western part of the island ("Western Landrige"). East of this borderline, the Ordovician limestone bedrock forms a flat plateau which slopes slightly south-eastwards down to the sea (e.g. STERNER & LUNDQVIST 1986). Compared to the other limestone areas in Northern Europe, the Ordovician limestone on Öland is hard with horizontal layers (e.g. KRAHULEC et al. 1986, STERNER & LUNDQVIST 1986). In most parts of the island, the bedrock is covered by quaternary deposits (e.g. STERNER &

LUNDQVIST 1986), but in the southern part, where the Great Alvar (> 200 km²) is located, these are relatively thin and partly absent. Here, a mosaic of different soil types occurs. Lime-poor moraine soils alternate with weathered soils of varying thicknesses originating from the limestone bedrock. Only a small part of the plateau consists of bare limestone, and in few cases karst phenomena can be found here (e.g. STERNER & LUNDQVIST 1986, KRAHULEC et al. 1986).

The climate of Öland shows both continental and oceanic traits. While the temperature regime is rather oceanic with a mean annual temperature of 7.0 °C (February -0.4 °C, July 16.6 °C, personal calculations for the period 1988–2001, data from the Ecological Station at the margin of the Great Alvar, Ölands Skogsby), the mean annual precipitation is relatively low, with about 450–500 mm in the coastal and central parts of the island (e.g. KRAHULEC et al. 1986, STERNER & LUNDQVIST 1986). Moreover, precipitation is especially low in summer and varies considerably from year to year with only slightly more than 300 mm in extremely dry years (KRAHULEC et al. 1986). Strong winds often intensify the desiccation of the thin soils in summer, whereas in autumn and spring the poor drainage of the compact limestone plateau leads in places to inundations. In winter, such water-saturated soils can be strongly affected by frost action (e.g. KÖNIGSSON 1968, ROSÉN 1982, KRAHULEC et al. 1986), leading partly to polygon soils and partly to a distinctive microrelief caused by frost-raising (ALBERTSON 1950).

The island was first colonised in the early Stone Age (e.g. ROSÉN 1982, ALM KÜBLER 2001), and the present-day thin soils of the Great Alvar are probably the result of soil erosion due to intensive grazing during the Bronze and Iron Ages and the early Medieval period (e.g. KÖNIGSSON 1968, DIERSSEN 1996). Grazing, small-scale agriculture and firewood cutting over many centuries have effectively kept back shrub- and woodland (KRAHULEC et al. 1986).

The alvar flora contains various taxa occurring as outliers far from their main distribution range, e.g. southeast European (steppe) species such as *Ranunculus illyricus*, south European species such as *Fumana procumbens* and *Globularia vulgaris*, Siberian species such as *Artemisia rupestris* and *Potentilla fruticosa*, and arctic-alpine species such as *Poa alpina* and many cryptogams (e.g. STERNER & LUNDQVIST 1986). In addition, one vascular plant species (*Galium oelandicum*) and several infraspecific taxa are endemic to the alvar vegetation of Öland. For an overview of the flora and vegetation of the island and the Great Alvar, see STERNER & LUNDQVIST (1986) and SJÖGREN (1988).

Our own study area comprises the northern part of southern Öland. The villages Färjestaden and N Möckleby form its northern corners, and Mörbylänga and Alby its southern corners (Fig. 1). Within this area, dry grassland communities of shallow, skeletal soils are mainly confined to thin weathered soils and bare rocks on the Ordovician limestone plateau. They grow on the Great Alvar as well as on the smaller alvar areas along the east coast. A few records also exist from the Western Landridge.

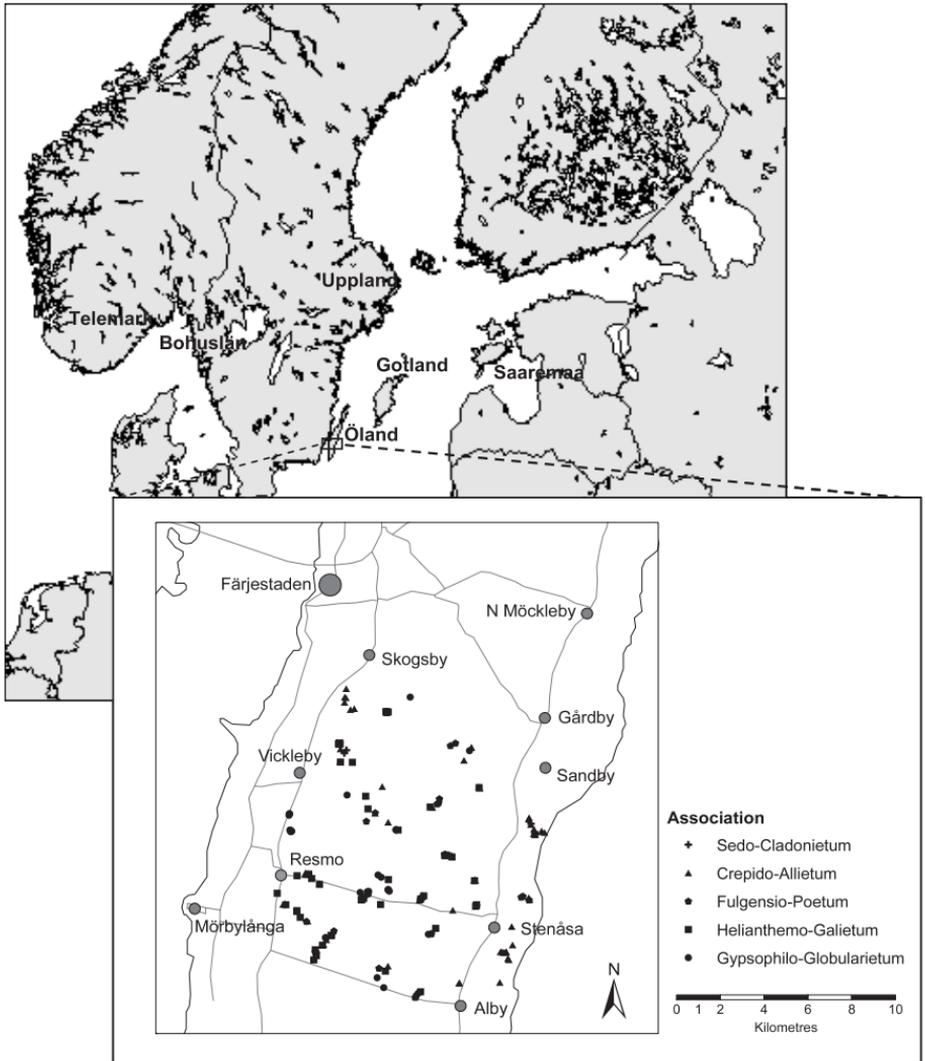


Fig. 1. Map of the southern parts of Northern Europe with delimitation of our own study area in southern Öland and indications of other regions with important *Alysso-Sedetalia* occurrences (either included in this study or discussed in 5.3). The inset map of southern Öland shows the distribution of the analysed plots of the *Alysso-Sedetalia* associations.

3 Material and methods

3.1 Plant nomenclature

In general, we use “*Flora Europaea*” (TUTIN et al. 1968–1993) for vascular plants, CORLEY et al. (1981) with the amendments by CORLEY & CRUND-

WELL (1991) for mosses, GROLLE & LONG (2000) for liverworts, and SANTESSON (1993) for lichens.

As an exception, we follow BLOM (1996, see also NYHOLM 1998) in the *Schistidium apocarpum* complex. Furthermore, we have introduced some additional species aggregates (agg.) to reflect less precise determinations (mainly from older literature): *Bryum bicolor* agg. and *B. capillare* agg. (both sensu FREY et al. 1995), *Racomitrium canescens* agg. (*R. canescens*, *R. elongatum*, *R. ericoides*), *Schistidium apocarpum* agg. (= *Schistidium apocarpum* complex sensu BLOM 1996), *Tortula ruralis* agg. (*T. calcicolens*, *T. ruraliformis*, *T. ruralis*), *Cladonia furcata* agg. (*C. furcata*, *C. scabriuscula*, *C. subrangiformis*), *Cladonia pyxidata* agg. (*C. chlorophaea*, *C. pyxidata*, to a small extent probably also *C. pocillum*). Finally, we recognise the following additional taxa because of their possible phytosociological importance: *Allium schoenoprasum* var. *alvarense* Hyl. and var. *schoenoprasum* (e.g. STERNER & LUNDQVIST 1986, JONSELL & KARLSSON 2004), *Arabis hirsuta* var. *glaberrima* Wg. and var. *hirsuta* (e.g. STERNER & LUNDQVIST 1986), *Silene uniflora* ssp. *petraea* (Fr. ex Hartm.) Jonsell & H. C. Prent. (e.g. JONSELL 2001), *Hypnum cupressiforme* var. *cupressiforme* and var. *lacunosum* Brid. (e.g. KOPERSKI et al. 2000), *Pottia conica* (Schwägr.) Nyholm (e.g. NYHOLM 1989) and *Tortula calcicolens* Kramer (e.g. NYHOLM 1989).

3.2 Relevés of southern Öland

During spring and summer 2001, we sampled 182 phytosociological relevés of dry grasslands growing on shallow, skeletal soils in the southern part of Öland (Fig. 1). The analysis included both very open rock vegetation dominated by cryptogams and communities on unstable soils, which are at least temporarily inundated and disturbed by frost action. Plots were distributed representatively over all the dry grasslands within the study area. Dry grassland sites were identified using topographical, geological and species distribution maps (STERNER & LUNDQVIST 1986).

All vascular plants, bryophytes and lichens (with the exception of epilithic crustose lichens) were identified. Abundance was estimated according to the Braun-Blanquet cover-abundance scale in the modified version of WILMANN'S (1998). Plots were 4 m² in size throughout, being a compromise between the usually very small plots (1 m² or less) proposed for pure cryptogam communities (e.g. DIERSCHKE 1994) and the larger plots (10–50 m²) used in most other dry grassland surveys.

For each relevé, several environmental and structural parameters were recorded. The soil depth (measured with a pointed iron rod, mean value of five randomly chosen positions), microtopography (maximum height difference between hummocks and hollows), cover of rocks, total and group specific cover of vegetation were all determined in the field. We took a mixed soil sample of the uppermost layer (0–10 cm) from different points of each plot. The samples were dried at 105 °C and their pH values measured with a pH-electrode (WTW) in distilled water. For a subset of these,

we also determined the content of organic matter as loss on ignition at 905 °C. This value was corrected for the carbon content measured by the Scheibler method (cf. SCHLICHTING et al. 1995). Mean moisture values (F-values, ELLENBERG et al. 1991) were calculated for each relevé by weighting the species with their coverage. Species not assessed by ELLENBERG et al. (1991) have been excluded but this applies only to a small proportion of all taxa.

3.3 Relevés from the literature

As bryophytes and lichens form a major part of the species composition of Sedo-Scleranthenea communities, we have only included relevés in which these taxa have been treated. In general, the classification and statistical evaluations should be based on even-sized plots (cf. JANDT & BRUELHEIDE 2002: 120, DENGLER 2003: 69). However, since this fact has rarely been considered in phytosociology, only a few relevés of equal plot size were available. We therefore decided to include relevés with plot sizes ranging from 2 to 10 m², i.e. those that are close to our own plot size of 4 m².

We have attempted to include all suitable records from Northern Europe ($n = 65$; see Appendix 3), except for those from southern Öland where we had sufficient own material. For the purpose of comparison, we have additionally collected literature relevés from different Alyso-Sedetalia communities in Central Europe (including the Alps), but with no attempt at completeness ($n = 127$; see Appendix 4). To avoid a predominance of the Poo compressae-Saxifragetum tridactylitae Géhu 1961 (*Saxifraga tridactylites*-community), we included only a subset of the numerous records of this community from anthropogenic sites such as railway gravel.

3.4 Statistical methods

3.4.1 Data preparation

Before applying numerical methods, we “standardised” the vegetation data to keep the effects of different floristic accuracy as small as possible:

(1) The following records were therefore eliminated: (i) non-epigeic species, because they have not been treated in the included literature; (ii) data for genera of which most of the included species were not determined (i.e. *Collema*, *Pottia*, *Riccia*, *Schistidium*, and *Bryum* except for *B. argenteum* and *B. capillare*); (iii) undetermined plants; (iv) records of species aggregates for which the micro-/subspecies have been determined in the majority of the relevés (i.e. *Festuca ovina* agg., *Phleum pratense*).

(2) Records were aggregated in the following cases: (i) cf.-data were assigned to the respective taxon; (ii) records were aggregated at the higher taxonomic level when determinations of different accuracies occurred in our data set; (iii) segregates not accepted in the used checklists (see 3.1) were assigned to the appropriate accepted taxon.

3.4.2 Cluster analyses

Cluster analyses were performed with the software SORT 4.0 (ACKERMANN & DURKA 1998). To obtain information about the data structure and ideas of possible classification schemes, we applied different cluster methods (average linkage, complete linkage) and various similarity and dissimilarity indices both to the complete data set and to subsets of it. For single relevés we preferred to use the Sørensen index, and for synoptic lists of syntaxa the Bray-Curtis index, a normalised derivate of the Euclidean distance (cf. ACKERMANN & DURKA 1998).

3.4.3 Ordinations

For ordination, we applied Detrended Correspondence Analysis (DCA, HILL & GAUCH 1980) with detrending by segments. DCA was performed on three different floristic data sets, (1) including all samples from both Northern and Central Europe, (2) including all samples from the Nordic countries, and (3) including only our own samples from Öland. In all cases, the length of the floristic gradient was > 4 standard deviations, indicating that unimodal-based ordination methods were appropriate for data analysis. Analyses were carried out using coverage classes transformed to their respective class means. No downweighting of rare species or transformation was applied.

For the data set consisting of our own samples from Öland, we examined the relationship between the floristic composition and the measured environmental variables indirectly, by relating environmental variables to extracted DCA axes using Spearman's Rank correlation. Ordinations were performed using the software package CANOCO 4.51 (TER BRAAK & ŠMILAUER 2002). Correlation analyses were carried out in SPSS.

3.4.4 Statistical tests

To test whether the Nordic communities differ in environmental and structural variables or species density, we used ANOVA (F -test). Tuckey's HSD test was applied for multiple comparisons among communities. When investigating species density, we included all relevés with a plot size of 4 m^2 (Northern Europe: $n = 199$; Central Europe: $n = 35$). When testing the associations of the alvar communities for their differences in vegetation structure and environmental conditions, we relied on our own relevés. ANOVA was carried out in SPSS.

3.5 Phytosociological methods

3.5.1 Classification principles

For the phytosociological classification, we took into account not only the different cluster analyses and ordinations but also various other data sour-

ces for regions or syntaxa not directly included in our study (synoptic tables, species lists, chorological data). Conceptually, we followed the application of the Braun-Blanquet approach proposed by DENGLER (2003, see also DENGLER & BERG 2002). This combines the ideas of BERGMIEIER et al. (1990) and the central syntaxon concept of DIERSCHKE (e.g. 1994: 324). We briefly outline only the most important aspects here (for detailed discussion and references, see DENGLER 2003):

- All species occurring within a plot are regarded as part of the whole phytocoenosis (= holocoenosis), including epigeic bryophytes and lichens but also epilithic and epiphytic taxa. In principle, these species groups are thus included in the relevés and are used for the syntaxonomic classification (due to determination problems, however, we had to refrain from taking into consideration epilithic crustose lichens in the present study).
- All phytocoenoses including so-called “atypical” or “fragmentary” types are taken into account for classification.
- The classification is carried out separately for three different structural types of vegetation: woodlands, herbaceous vegetation (including dwarf shrubs) and one-layered cryptogam vegetation. This means that, for example, a moss species can be considered as characteristic for one syntaxon in each of these three types.
- The presence reference values (in short: presence degrees) of syntaxa above the association level are calculated as means of the presence degrees of all the associations belonging to them.
- The presence degree of a differential species has to be at least twice as high as in the syntaxon from which it has to be separated. A character species has to fulfil this criterion compared with all other syntaxa of equal rank within the same structural type.
- Exceptionally, one taxon can be considered as a character species of two (or more) syntaxa of the same structural type if the ranges of their next superior syntaxa do not overlap.
- “Transgressive character species” meet the character species criterion within several intercalated syntaxa.
- Within each syntaxon of superior rank, one “central syntaxon” can be described which is characterised by diagnostic species of the syntaxonomic level(s) above, but has insufficient or no character species of its own. As a result, informal (“unranked”) communities become superfluous.

In our study, we have only analysed phytocoenoses of the herbaceous vegetation. A stand was included if the total cover of the herb layer reached 5% or if the number of vascular plant “individuals” together was at least 50 (2m) on 4 m²; otherwise we regarded it as belonging to the cryptogam vegetation.

To evaluate whether a certain taxon can be considered as a character species, an estimate of its presence degrees in syntaxa not treated in this paper was necessary. For this purpose, we used different sources of information, especially the comprehensive synoptic tables of southern Germany

(OBERDORFER 1992, 1993a, 1993b), the Netherlands (SCHAMINÉE et al. 1995, 1996a, 1998, STORTELDER et al. 1999), Northern Europe (DIERSSEN 1996) and Mecklenburg-Vorpommern (northeast Germany; BERG et al. 2001). In addition, we consulted unpublished synoptic tables of the herbaceous xerothermic vegetation of Europe compiled from numerous sources by the first author.

3.5.2 Vegetation table

In the synoptic table (Table 1), we present presence (reference) values (see 3.5.1) for the Nordic syntaxa from association to alliance level. For the purpose of comparison, we also illustrate the Central European alliance by a column. Since its subdivision into associations according to the described classification principles is unclear, presence degrees here were calculated on the basis of relevés instead of associations. The diagnostic value of the different taxa is illustrated by the use of shadings and frames as suggested by BERG et al. (2001).

3.5.3 Phytosociological nomenclature

The naming of the syntaxa follows the International Code of Phytosociological Nomenclature (WEBER et al. 2000; referred to below as ICPN). In Table 5, all the syntaxa which are treated in more detail are listed in their hierarchical order with their full names and author citations. We give author citations in the text only for syntaxa not included in this overview and when they are used for the first time. Syntaxa for which no valid and legitimate names were available are described as new. These new descriptions or namings as well as the necessary typifications are presented in Appendix 1. Major synonyms (if necessary with an indication of the relevant ICPN Article according to which they are invalid or illegitimate) are also given there (for details of the presentation, see DENGLER et al. 2003). The newly designated type relevés of associations are listed in Appendix 2. We have checked the sources for the author citations of all syntaxa cited in the nomenclatural overview and appendix and have included them in the reference list.

4 Results

4.1 Characterisation of the Nordic communities

We were able to distinguish six community types at the association level when aggregating the relevés of the Nordic data set until the units obtained conformed to the criteria of section 3.5.1 (Table 1).

4.1.1 *Cladonio symphycaepae-Sedetum albi*

Floristic composition: The *Cladonio-Sedetum* comprises poorly characterised stands dominated by *Sedum acre* and *S. album*. The vascular

plants, among them several therophytes such as *Saxifraga tridactylites* and *Erophila verna*, mostly grow on moss cushions often dominated by *Tortula ruralis* agg. Many of the alvar-specific cryptogams are absent, whereas more acidophilous species such as *Ceratodon purpureus* occur. *Allium oleraceum*, *Silene nutans* and *Poa compressa* differentiate the association. The community generally occurs in very small patches, leading to a varying floristic composition depending on the adjacent plant community. Records from Norway (MARKER 1969) are rich in *Poa alpina*; their overall floristic composition, however, is very distinct from that of the Fulgensio-Poetum (see 4.1.4) of the Ölandic alvar.

Ecology and distribution: In Norway, MARKER (1969) recorded the community from bare rocks or shallow soils over shell deposits and limestone bedrock. On southern Öland, it occurs only rarely. We found it twice on the margins of the Great Alvar and once in a small alvar area in the east, both on bare limestone bedrock and on gravel deposits. In all cases, the sites were sun exposed, with very thin soil layers. Further relevés originate from shore ridges in northern Öland (DENGLER & RIXEN unpubl. report 1995) and from a small Baltic island in the province of Uppland (TÜXEN 1951).

4.1.2 *Ditricho flexicaulis*-*Sedetum acris*

Floristic composition: The association is characterised by a very special cryptogam flora, including *Tortella fragilis*, *Catapyrenium cinereum* and *Bacidia bagliettoana*, which may serve as character species. However, the dominant components of the cryptogam layer are generally *Tortella tortuosa* and *Ditrichum flexicaule*, the latter especially occurring on slightly deeper soils (HALLBERG 1971). The association was found close to the sea coast and thus hosts some “maritime” taxa such as *Armeria maritima* ssp. *maritima*, which differentiate it from the other communities of the alliance. Compared to these, the community also contains a relatively high number of mesophilous species (e.g. *Festuca rubra*, *Achillea millefolium*, *Lotus corniculatus*).

Ecology and distribution: All the included relevés originate from Bohuslän on the Swedish west coast (HALLBERG 1971). In contrast to the *Cladonio-Sedetum* (see 4.1.1), the *Ditricho-Sedetum* does not occur on limestone but on acidic rocks covered by shallow soils or even on sand and

Table 1 (opposite). Abridged synoptic table of the *Alysso-Sedetalia* syntaxa in Northern Europe (All. 2) compared with those of Central Europe (All. 1). The two suballiances and six associations belonging to the Nordic *Tortello tortuosae*-*Sedion albi* are also represented by columns. For the numbers of the syntaxa, see Table 5. The numbers in the columns indicate the percentage presence degrees of the respective taxa. Only diagnostic taxa and companion taxa with a mean presence degree of more than 8% in the two alliances are shown.

- = character species of an alliance, suballiance or association
- = character species of the order or superior rank of a transgressive character species
- = differential species
- = negatively differentiating species within a species block

- V = vascular plant
- B = bryophyte
- L = lichen
- A = "alga"

Syntaxon	All. 1	All. 2	Suball. 2a	Suball. 2b	2.1	2.2	2.3	2.4	2.5	2.6
Number of relevés	127	247	64	183	21	43	75	25	43	40
Mean number of plant taxa (total)	18	44	36	49	28	43	42	48	51	53
Mean number of vascular plants	13	19	20	19	18	21	19	12	20	23
Mean number of bryophytes	3	16	10	19	7	12	18	23	18	18
Mean number of lichens	2	9	6	11	3	10	5	13	13	11

Ord. - <i>Alyso alyssoides</i> - <i>Sedetalia</i>	V	B	L	A	2.1	2.2	2.3	2.4	2.5	2.6	
<i>Arenaria serpyllifolia</i> (total, see also all. 1)	V	67	55	82	42	76	88	21	32	70	43
<i>Acinos arvensis</i>	V	30	57	50	60	62	37	59	48	60	73
<i>Cladonia symphyrcarpa</i>	L	16	55	45	60	52	37	35	92	62	50

All. 1 - <i>Alyso alyssoides</i> - <i>Sedion</i> (central alliance)											
C	<i>Arenaria serpyllifolia</i> ssp. <i>leptoclados</i>	V	27
Ord.	<i>Thlaspi perfoliatum</i>	V	17	4	7	2	14	.	.	8	.
	<i>Minuartia mutabilis</i>	V	6
	<i>Minuartia hybrida</i>	V	2
	<i>Cerastium brachypetalum</i>	V	1
	<i>Minuartia glomerata</i> ssp. <i>glomerata</i>	V	1
D	<i>Sedum sexangulare</i>	V	29	0.3	2	.
	<i>Medicago minima</i>	V	24
	<i>Alyssum alyssoides</i>	V	23
	<i>Petrorhagia saxifraga</i>	V	22
	<i>Poa perconcinna</i>	V	20

All. 2 - <i>Tortello tortuosae</i> - <i>Sedion albi</i>												
C	Ord. <i>Ditrichum flexicaule</i>	B	12	75	58	83	48	67	76	88	79	90
	<i>Cladonia pocillum</i>	L	2	40	51	35	29	72	17	24	44	53
	<i>Encalypta rhytocarpa</i>	B	.	15	14	16	5	23	12	28	14	10
D	<i>Festuca ovina</i>	V	.	79	75	81	71	79	76	56	100	93
	<i>Tortella tortuosa</i>	B	4	78	59	88	52	65	76	100	89	85
	<i>Barbula convoluta</i>	B	9	58	53	61	19	86	68	56	60	60
Ci.	<i>Cladonia rangiformis</i>	L	3	52	47	55	29	65	33	28	76	83
	<i>Galium verum</i> ssp. <i>verum</i>	V	2	51	73	40	57	88	33	12	44	70
	<i>Anthyllis vulneraria</i>	V	2	49	65	41	43	86	34	4	39	88
	<i>Medicago lupulina</i>	V	6	41	28	48	29	26	31	40	60	60
	<i>Bromus hordeaceus</i> ssp. <i>hordeaceus</i>	V	8	38	46	34	52	40	31	60	38	5
	<i>Homalothecium lutescens</i>	B	1	36	33	38	19	47	36	24	42	50
	<i>Linum catharticum</i>	V	.	36	25	41	14	35	67	12	51	35
	<i>Bryum capillare</i>	B	.	33	27	37	24	30	15	48	35	48
	<i>Bryoerythrophyllum recurvirostrum</i>	B	1	33	36	32	.	72	20	48	28	30
	<i>Leptogium lichenooides</i>	L	.	26	25	26	.	49	16	60	21	8
	<i>Arabis hirsuta</i> (total, see also ass. 2.6)	V	.	22	29	19	29	28	24	4	12	35

Suball. 2a - <i>Tortello tortuosae</i> - <i>Sedion albi</i> (central suballiance)												
D	Ci. <i>Ceratodon purpureus</i>	B	42	28	52	16	38	65	13	16	23	13
	<i>Cladonia furcata</i>	L	2	24	52	10	19	84	5	4	19	10
	Ci. <i>Cerastium semidecandrum</i>	V	24	18	45	4	29	60	3	.	14	.
Subcl.	<i>Potentilla argentea</i> agg.	V	12	15	35	5	33	37	5	.	12	3
	<i>Homalothecium sericeum</i>	B	2	12	25	6	24	26	1	4	9	10
	<i>Encalypta streptocarpa</i>	B	4	10	24	4	14	33	3	8	.	3

Ass. 2.1 - <i>Cladonia symphyrcarpae</i> - <i>Sedetum albi</i>												
D	<i>Allium oleraceum</i>	V	6	12	34	1	62	5	.	.	2	3
	<i>Poa compressa</i>	V	21	21	35	14	57	12	23	4	16	13
Ord.	<i>Saxifraga tridactylites</i>	V	31	39	31	43	48	14	27	80	28	35
	<i>Silene nutans</i> ssp. <i>nutans</i>	V	1	9	15	6	24	5	.	.	9	15

Ass. 2.2 - <i>Ditricho flexicaulis</i> - <i>Sedetum acris</i>												
C	<i>Bacidia bagliettoana</i>	L	.	16	30	9	.	60	9	.	12	15
	<i>Tortella fragilis</i>	B	.	13	29	4	.	58	15	.	2	.
	<i>Catapyrenium cinereum</i>	L	.	6	18	1	.	35	.	.	2	.
D	<i>Festuca rubra</i>	V	2	16	44	2	10	77	8	.	.	.
	<i>Achillea millefolium</i> ssp. <i>millefolium</i>	V	2	17	35	8	10	60	23	.	7	.
	<i>Lotus corniculatus</i>	V	2	16	30	9	10	49	29	.	5	3
	<i>Taraxacum obliquum</i> agg.	V	.	8	24	0	.	47
	<i>Antennaria dioica</i>	V	.	9	22	2	.	44	1	.	5	3
	<i>Erigeron acer</i>	V	2	7	22	0	.	44
	<i>Pimpinella saxifraga</i>	V	2	9	25	1	5	44	.	.	.	3
	<i>Armeria maritima</i> ssp. <i>maritima</i>	V	.	8	25	0	10	40
Ci.	<i>Agrostis vinealis</i>	V	.	8	18	3	.	35	3	.	7	3
Ci.	<i>Racomitrium canescens</i> agg.	B	16	12	22	7	10	33	4	8	7	10

Table 1 (cont.)

Syntaxon		All. 1	All. 2	Suball.	Suball.	2.1	2.2	2.3	2.4	2.5	2.6
Number of relevés		127	247	2a	2b	21	43	75	25	43	40
Caloplaca cerina	L	.	5	15	0	.	30
Carex caryophyllea	V	.	6	15	2	.	30	1	.	.	5
Poa pratensis agg.	V	3	9	20	4	10	30	8	.	5	3
Euphrasia nemorosa	V	.	5	14	0	.	28
Leptogium gelatinosum	L	.	10	14	9	.	28	8	24	2	.
Botrychium lunaria	V	.	4	12	0	.	23
Luzula campestris	V	.	5	14	0	5	23
Viola tricolor	V	.	4	12	1	.	23	.	.	2	.
Solidago virgaurea	V	.	4	11	1	.	21	.	.	.	3
Suball. 2b - Tortello rigentis-Helianthemion oelandici											
C											
Cladonia subrangiformis	L	.	38	.	57	.	.	13	48	81	85
Encalypta vulgaris	B	.	35	.	53	.	.	39	64	47	60
Allium schoenoprasum var. alvarense	V	.	31	.	46	.	.	68	68	25	23
Helianthemum oelandicum ssp. oelandicum	V	.	29	.	44	.	.	7	12	72	83
Trichostomum crispulum	B	.	29	.	44	.	.	39	44	51	40
Distichium capillaceum	B	.	32	11	42	5	16	37	52	49	30
Ord. Hornungia petraea	V	6	31	7	43	14	.	8	56	56	50
Tortella rigens	B	.	26	.	39	.	.	45	48	32	30
Didymodon ferrugineus	B	.	23	3	33	5	.	35	56	26	13
Didymodon rigidulus	B	.	21	.	31	.	.	25	68	19	13
Athalamia hyalina	B	.	16	3	22	5	.	25	16	28	20
Festuca oelandica	V	.	13	3	19	5	.	39	24	9	3
Gymnostomum aeruginosum	B	.	11	.	16	.	.	23	20	9	13
Leptogium schraderi	L	.	10	.	16	.	.	11	24	19	8
Silene uniflora ssp. petraea	V	.	3	.	5	.	.	.	8	5	5
Hieracium x dichotomum	V	.	2	.	3	.	.	5	.	2	3
D											
Ci. Thymus serpyllum ssp. serpyllum	V	.	45	3	66	5	.	37	52	86	88
Ord. Tortella inclinata	B	28	40	.	60	.	.	33	88	58	60
Didymodon fallax	B	3	41	7	58	5	9	51	76	60	45
Fissidens dubius	B	.	39	13	53	10	16	71	4	65	70
Weissia brachycarpa (incl. cf. data)	B	.	35	.	52	.	.	46	52	47	63
Agrostis stolonifera	V	.	35	1	52	.	2	96	44	53	13
Scorpidium turgescens	B	.	30	3	44	5	.	61	56	39	18
Ord. Cerastium pumilum	V	16	30	7	42	14	.	35	56	47	30
Pleuroidium acuminatum (incl. cf. data)	B	.	26	.	40	.	.	34	60	39	25
Campyllum chrysophyllum	B	.	26	3	38	.	5	55	20	44	33
Ord. Psora decipiens	L	12	22	.	33	.	.	16	56	37	23
Thamnia vermicularis var. subuliformis	L	.	21	.	31	20	47
Myurella julacea	B	.	18	1	27	.	2	33	32	21	20
Filipendula vulgaris	V	.	18	1	26	.	2	19	4	31	50
Ctenidium molluscum	B	.	15	3	21	.	5	27	24	23	10
Pseudocrossidium hornschuchianum	B	3	14	.	21	.	.	12	36	26	10
Ass. 2.3 - Crepido pumilae-Allietum alvarensis											
C											
Crepis tectorum ssp. pumila	V	.	19	.	29	.	.	61	28	26	.
Artemisia rupestris	V	.	5	.	7	.	.	19	.	2	8
D											
Prunella vulgaris	V	.	20	16	23	24	7	71	4	12	3
Sagina nodosa	V	.	22	26	21	14	37	57	20	5	.
Leontodon autumnalis	V	.	16	14	16	.	28	41	12	7	5
Drepanocladus cossonii	B	.	8	.	12	.	.	36	.	7	3
Calliergonella cuspidata	B	.	5	.	8	.	.	29	.	2	.
Eucladium verticillatum	B	.	10	.	14	.	.	25	12	12	8
Phleum pratense ssp. bertolonii	V	.	6	3	8	5	.	23	4	5	.
Rumex acetosella	V	8	7	6	7	.	12	23	.	5	.
D Ass. 2.3 and 2.4 (against 2.5 and 2.6)											
Nostoc sp.	A	.	28	21	31	5	37	48	56	14	5
D. Ass. 2.3, 2.5 and 2.6 (against 2.4)											
Ci. Taraxacum erythrospermum agg.	V	17	31	30	31	24	35	20	8	44	53
Taraxacum officinale agg.	V	9	20	3	29	5	.	24	8	32	50
Plantago lanceolata	V	9	31	51	21	38	63	37	.	28	20
Ass. 2.4 - Fulgensio bracteatae-Poetum alpinae											
C											
Fulgensia bracteata	L	2	26	.	39	.	.	21	84	32	20
Ord. Toninia sedifolia	L	15	22	6	31	.	12	15	76	23	8
Tortula calcicolens	B	.	21	3	30	5	.	9	76	16	20
Lecidea lurida	L	.	21	.	31	.	.	19	68	26	10
Schistidium atrofussum	B	.	15	.	22	.	.	16	56	5	10
Fulgensia fulgens	L	14	10	.	14	.	.	7	40	7	3
Tortella densa	B	.	12	.	18	.	.	12	40	14	5
Ceratodon conicus	B	.	7	.	11	.	.	5	28	7	3
Squamarina cartilaginea	L	.	3	.	4	16	.
Squamarina lentigera	L	.	3	.	4	.	.	1	12	2	.
D											
Poa alpina	V	.	28	36	25	71	.	13	76	7	3

Table 1 (cont.)

Syntaxon		All. 1	All. 2	Suball. 2a	Suball. 2b	2.1	2.2	2.3	2.4	2.5	2.6
Number of relevés		127	247	64	183	21	43	75	25	43	40
<i>Tortula ruraliformis</i>	B	.	22	7	30	14	.	11	64	9	35
<i>Collema cristatum</i>	L	.	13	.	19	.	.	8	60	.	8
<i>Collema crispum</i>	L	.	15	.	22	.	.	13	52	14	8
<i>Bryum argenteum</i>	B	14	21	26	19	24	28	4	48	9	13
Ass. 2.5 - Helianthemo oelandici-Galietum oelandici											
C											
<i>Galium oelandicum</i>	V	.	9	.	13	.	.	9	.	37	5
<i>Sisymbrium supinum</i>	V	.	4	.	6	.	.	5	4	16	.
D											
<i>Anthoxanthum odoratum</i>	V	.	10	11	10	.	21	9	.	21	10
D. Ass. 2.5 and 2.6 (against 2.3 and 2.4)											
<i>Cetraria islandica</i>	L	5	38	22	46	14	30	11	16	68	88
Cl. <i>Cetraria aculeata</i>	L	9	37	38	37	10	65	4	8	63	73
Subcl. <i>Cladonia foliacea</i>	L	16	40	40	40	10	70	15	20	65	60
<i>Artemisia campestris</i> ssp. <i>campestris</i>	V	5	36	37	36	67	7	12	20	42	70
Subcl. <i>Potentilla tabernaemontani</i>	V	14	23	5	32	10	.	8	12	49	60
<i>Hieracium pilosella</i>	V	12	35	47	30	24	70	12	4	44	58
<i>Cephaloziella divaricata</i>	B	1	20	.	30	.	.	19	4	47	50
<i>Cetraria ericetorum</i> ssp. <i>ericetorum</i>	L	.	19	5	26	5	5	1	4	44	53
<i>Cetraria nivalis</i>	L	.	13	.	19	28	48
<i>Scapania calcicola</i>	B	.	15	.	22	.	.	9	8	32	40
<i>Campanula rotundifolia</i>	V	1	20	20	21	10	30	7	4	31	40
<i>Dicranum scoparium</i>	B	2	18	10	22	14	5	16	.	32	38
Subcl. <i>Sedum rupestre</i>	V	5	14	7	17	14	.	8	.	32	28
<i>Hypogymnia physodes</i>	L	.	13	16	12	10	21	.	.	21	25
Ass. 2.6 - Gypsophilo fastigiatae-Globularietum vulgaris											
C											
<i>Globularia vulgaris</i>	V	.	13	.	19	2	73
<i>Gypsophila fastigiata</i>	V	.	13	.	19	.	.	.	8	7	60
<i>Arabis hirsuta</i> var. <i>glaberrima</i>	V	.	8	3	11	5	.	4	4	7	28
D											
<i>Vincetoxicum hircundinaria</i> ssp. <i>hirundin.</i>	V	.	15	7	20	14	.	1	.	12	65
<i>Asperula tinctoria</i>	V	.	11	.	17	.	.	1	.	16	50
<i>Rhytidium rugosum</i>	B	9	18	13	21	24	2	8	8	16	50
<i>Avenula pratensis</i> ssp. <i>pratensis</i>	V	2	20	22	19	29	14	7	.	19	48
<i>Grimmia pulvinata</i>	B	6	16	10	19	19	.	3	16	16	40
<i>Melica ciliata</i> ssp. <i>ciliata</i>	V	5	7	.	11	9	35
<i>Oxytropis campestris</i> ssp. <i>campestris</i>	V	.	6	3	8	5	.	.	.	2	30
<i>Carex ericetorum</i>	V	.	7	7	7	14	.	1	.	.	28
<i>Agrostis gigantea</i> ssp. <i>gigantea</i>	V	.	7	.	10	.	.	3	4	7	25
<i>Cladonia convoluta</i>	L	10	7	3	9	5	.	3	4	7	23
<i>Galium boreale</i>	V	.	5	.	7	.	.	1	.	7	20
<i>Pulsatilla pratensis</i> ssp. <i>pratensis</i>	V	.	5	.	7	7	20
Subcl. - Sedo-Scleranthenea											
<i>Sedum album</i>	V	36	75	57	84	90	23	71	96	84	83
<i>Erophila verna</i>	V	32	40	24	47	29	19	37	72	42	38
<i>Peltigera rufescens</i>	L	14	42	63	31	38	88	27	40	32	25
<i>Bryum caespiticium</i> (incl. cf. data)	B	10	17	3	24	5	.	19	32	26	20
<i>Bryum elegans</i>	B	.	21	3	31	5	.	45	36	21	20
<i>Sempervivum arachnoideum</i>	V	17
<i>Peltigera didactyla</i>	L	.	11	5	14	10	.	11	24	17	3
Cl. - Koelerio-Corynephoretea											
<i>Tortula ruralis</i> agg. (total, also see ass. 2.5)	B	40	53	71	44	76	65	16	88	26	45
<i>Sedum acre</i>	V	30	58	88	43	95	81	36	40	39	58
<i>Cladonia furcata</i> agg. (total, also see suball. 2a and 2b)	L	1	46	43	47	15	70	17	0	81	90
Other species: vascular plants											
<i>Veronica arvensis</i>	V	19	4	10	2	14	5	7	.	.	.
<i>Erodium cicutarium</i> ssp. <i>cuticularium</i>	V	18	4	11	1	14	7	3	.	2	.
<i>Arabidopsis thaliana</i>	V	17	1	4	0	.	7	1	.	.	.
<i>Thymus praecox</i> ssp. <i>praecox</i>	V	18	0	.	0
<i>Hypericum perforatum</i>	V	10	7	3	9	5	.	5	4	12	13
Other species: epigeic bryophytes											
<i>Hypnum cupressiforme</i> (mainly var. <i>lacunosum</i>)	B	23	80	79	80	71	86	52	88	86	95
<i>Bryum</i> sp.	B	9	52	61	48	38	84	56	40	51	43
<i>Thuidium abietinum</i>	B	14	44	67	32	62	72	40	32	26	30
Other species: epigeic lichens											
<i>Cladonia pyxidata</i> agg.	L	13	25	28	24	19	37	17	.	31	48
<i>Collema</i> sp.	L	5	23	28	21	.	56	23	20	26	15

gravel deposits which are secondarily enriched with a base-rich material from shell deposits (HALLBERG 1971). The community sometimes even grows close to the beach line, where some fertilisation due to bird dung may have occurred (HALLBERG 1971). The sites are sun- and wind-exposed and thus very dry in summer, but they are sometimes inundated in winter (HALLBERG 1971).

4.1.3 *Crepido pumilae*-*Allietum alvarensis*

Floristic composition: This community shows a peculiar mixture of xerophilous and hygrophilous elements. It is characterised by *Crepis tectorum* ssp. *pumila*, an Öland endemic (JONSELL & KARLSSON 2004), and the continentally distributed *Artemisia rupestris*. The field layer of the *Crepido*-*Allietum* is relatively dense and is dominated by the graminoids *Agrostis stolonifera*, *Festuca ovina* and the Öland endemic *Festuca oelandica*. Several taxa indicating loamy soils such as *Leontodon autumnalis*, *Prunella vulgaris* and *Sagina nodosa* differentiate the association. In addition to typical species of the alvar dry grasslands of shallow, skeletal soils, the cryptogam layer contains bryophytes which otherwise occur in rich-fen communities, as for example *Calliergonella cuspidata* and *Drepanocladus cossonii*. The *Crepido*-*Allietum* also includes several species typical for heavily grazed meadows and “weeds” such as *Chaenorrhinum minus*, *Convolvulus arvensis* and *Linaria vulgaris*. These are probably indigenous on the Great Alvar (STERNER & LUNDQVIST 1986).

Ecology and distribution: The community occurs on shallow loamy soils with an average depth of 7 cm. Soils are often poorly drained and are affected by frost action, leading to polygon structures with assorted material or, more often, to soil tufts which may be intensified by trampling cattle (e.g. STERNER & LUNDQVIST 1986). In contrast to the following community, the cover of bare rock is generally low. The opposing forces of drought in summer and waterlogging in winter together with the mechanical stress of frost action explain the special species combination. On Öland, the community occurs both on the Great Alvar and in the smaller alvar areas on the east coast. Only one relevé from outside Öland was available, originating from the little island of Stora Karlsö near Gotland (WESTHOFF et al. 1983). This stand, dominated by *Artemisia rupestris*, however, shows a species density more than three times lower than in our relevés, which may be due to an incomplete species list.

4.1.4 *Fulgensio bracteatae*-*Poetum alpinae* (Fig. 2)

Floristic composition: The *Fulgensio*-*Poetum* is clearly distinct from the *Crepido*-*Allietum* (4.1.3) as regards community structure, floristic composition and site conditions. It is characterised by its rich cryptogam flora, especially the crustose lichens *Fulgensia bracteata*, *F. fulgens*, *Toninia sedifolia* and *Lecidea lurida*. *Schistidium atrofusum*, *Tortella calcicolens* and



Fig. 2. The *Fulgensio bracteatae*-*Poetum alpinae* inhabiting bare limestone bedrock in the Great Alvar of Öland. On the moss cushions, mostly formed by *Ditrichum flexicaule* and *Tortella* species, *Sedum album*, *Allium schoenoprasum* var. *alvarense* and the lichen *Fulgensia bracteata* grow (photograph: J. Dengler, 05/1994).

Ceratodon conicus are characteristic moss species. Vascular plants are relatively unimportant for the community structure (mean cover 18.3%). Among these, *Sedum album* attains the highest degrees of cover. In addition, several small therophytes, especially *Arenaria serpyllifolia*, *Erophila verna* and *Saxifraga tridactylites*, colonise the moss cushions. *Poa alpina* differentiates the community from the others alvar communities.

Ecology and distribution: The community is the first vascular plant association to colonise bare rocks and extremely shallow soils. During the succession, the small moss cushions grow together and accumulate more and more soil beneath. This soil is rich in organic matter (mean 20.1%). Due to erosion by wind and water as well as trampling livestock, the community probably stays open over quite long periods. The community is much less affected by inundation and frost action than the *Crepido-Allietum* (4.1.3). Only relevés from Öland were available, where the community mainly grows in the Great Alvar but rarely also in some small alvar regions on the east coast.

4.1.5 *Helianthemo oelandici*-*Galietum oelandici*

Floristic composition: The flowering aspect of the community is dominated by the dwarf shrubs *Thymus serpyllum* (widely distributed) and the

Öland endemic *Helianthemum oelandicum* ssp. *oelandicum* (jointly with the Gypsophilo-Globularietum, see 4.1.6). Floristically, the association is poorly characterised. *Galium oelandicum* and *Sisymbrium supinum* are probably the sole character species, but only gain low to intermediate presence degrees. KRAHULEC et al. (1986) mention *Hieracium ×dichotomum* as a further potential character species, but our own data do not support this. The cryptogam layer is characterised by several fruticose lichens. Among these are the arctic-alpine species *Thamnolia vermicularis*, *Cetraria nivalis* and *C. cucullata* which are shared with the Gypsophilo-Globularietum (4.1.6).

Ecology and distribution: The community occurs on sites with slightly deeper soils (mean 5.7 cm) than the Fulgensio-Poetum (4.1.4), probably following it in succession when the vegetation becomes closer. Ecologically, the community is intermediate between the Crepido-Allietum (4.1.3) and the Gypsophilo-Globularietum (4.1.6). In southern Öland the community occurs all over the Great Alvar, often covering huge areas, but it was only rarely found in the small alvar areas along the east coast. Two relevés from Gotland by DU RIETZ (1925) were included due to their overall species composition, though the name-giving species were missing.

4.1.6 *Gypsophilo fastigiatae*-*Globularietum vulgaris* (Fig. 3)

Floristic composition: With an average of 53.6 species on 4 m², the Gypsophilo-Globularietum is the weathered rock community with the highest species density in Northern Europe (see Table 4). The community is characterised by the south-western *Globularia vulgaris*, whose major distribution range is in southern France and northern Spain, and the south-eastern *Gypsophila fastigiata*. Other southeastern plants differentiating it from the Helianthemo-Galietum (4.1.5) are *Vincetoxicum hirundinaria*, *Melica ciliata* and *Oxytropis campestris*. Species indicating moist soil conditions are absent; *Agrostis stolonifera* is replaced by *A. gigantea*. Finally, glabrous individuals of *Arabis hirsuta* are found most frequently in this association. They would become a third character taxon, if accepted as a valid entity (var. *glaberrima*, see 3.1). The composition of the cryptogam layer is quite similar to that of the Helianthemo-Galietum (4.1.5) but with *Rhytidium rugosum* and *Grimmia pulvinata* as differential species.

Ecology and distribution: The community occurs on shallow soils of varying depths due to many fissures in the limestone bedrock. The soil is very fine and rich in organic matter (mean 22.7%), with a deep brown-black colour. Soils are well drained and are not at all affected by inundation and frost action; fine soil accumulations in rock fissures may even be more resistant against drying out in summer. On Öland, the community occurs exclusively on the Great Alvar, often in karst areas. It normally covers relatively small areas which are interspersed with small groups of *Juniperus communis* shrubs that are colonising deeper fissures in the bedrock, espe-



Fig. 3. The *Gypsophilo fastigiatae*-*Globularietum vulgaris* on the Great Alvar of Öland. *Globularia vulgaris*, *Oxytropis campestris* ssp. *campestris*, *Pulsatilla pratensis* ssp. *pratensis* and the lichen *Thamnolia vermicularis* are shown. This association is the geographically most restricted of the alliance *Tortello tortuosae*-*Sedio albi*. It is endemic to Öland, Stora Karlsö and Gotland. With a mean of 53.6 species on 4 m², it is the most species-rich association (photograph: J. Dengler, 05/1994).

cially when grazing intensity is low. Sites are often threatened by overgrowing. One relevé from Stora Karlsö near Gotland by WESTHOFF et al. (1983) also belongs to this association.

4.2 Cluster analyses

When cluster analyses were applied to the whole data set of 372 relevés, the Nordic and the Central European records were well separated. The results were very similar for the different methods tested. Using the Sørensen similarity index and average linkage, only one Central European relevé was grouped together with the Northern European relevés and none of these relevés with the Central European ones.

Analysing only the Nordic relevés, no clear bipartition became obvious. However, apart from a few exceptions, the major branches of the dendrogram consisted either of relevés from southern Öland or of relevés from other regions. Those relevés forming an exception were, on the one hand, a few relevés from disturbed or marginal alvar sites in southern Öland

which repeatedly clustered with relevés from other regions and, on the other hand, two relevés from Gotlandic alvar sites which could sometimes be found within an Öland alvar cluster.

4.3 Ordinations

The DCA diagram (Fig. 4) reveals a clear floristic distinction between the Central and Northern European communities. Communities of the Scandinavian mainland are intermediate between the Ölandic alvar communities and those of Central Europe. In contrast to the Central European communities, the Nordic communities show a relatively homogeneous floristic composition. There seem to be two rather distinct subgroups among the Central European communities. Relevés in the upper part of the graph

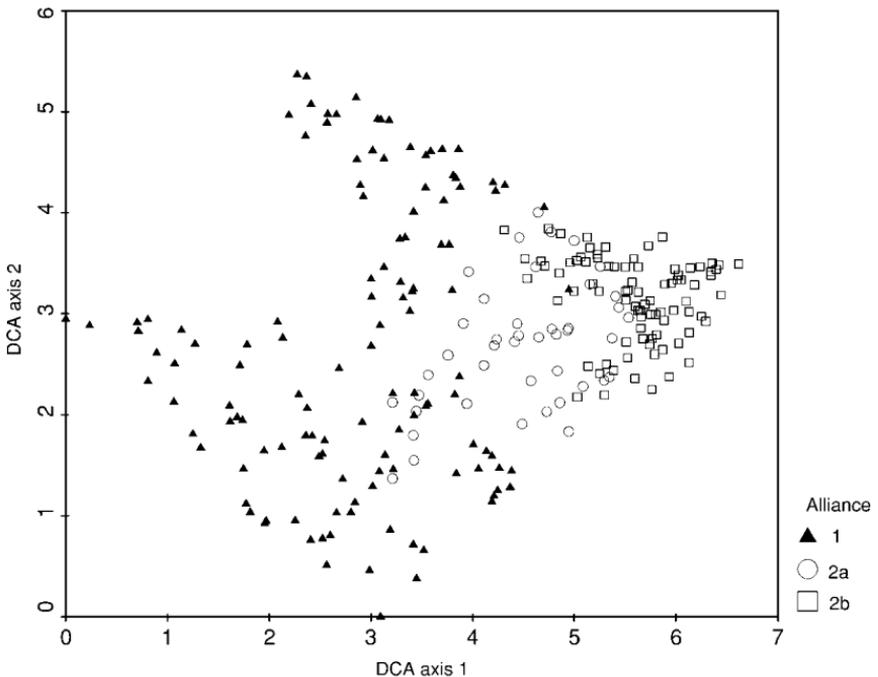


Fig. 4. Ordination diagram with axes 1 and 2 of a DCA revealing the floristic relationships between relevés belonging to the Central European alliance *Alysso-Sedion* (1) and the Northern European relevés assigned to the alliance *Tortello tortuosae-Sedion albi* (2), with the suballiances *Tortello tortuosae-Sedion albi* (2a: *Cladonio-Sedetum* and *Ditricho-Sedetum*), mostly comprising communities on the Scandinavian mainland, and *Tortello rigentis-Helianthemion oelandici* (2b: other associations), mostly comprising Ölandic alvar communities (Eigenvalues: axis 1: 0.719, axis 2: 0.614).

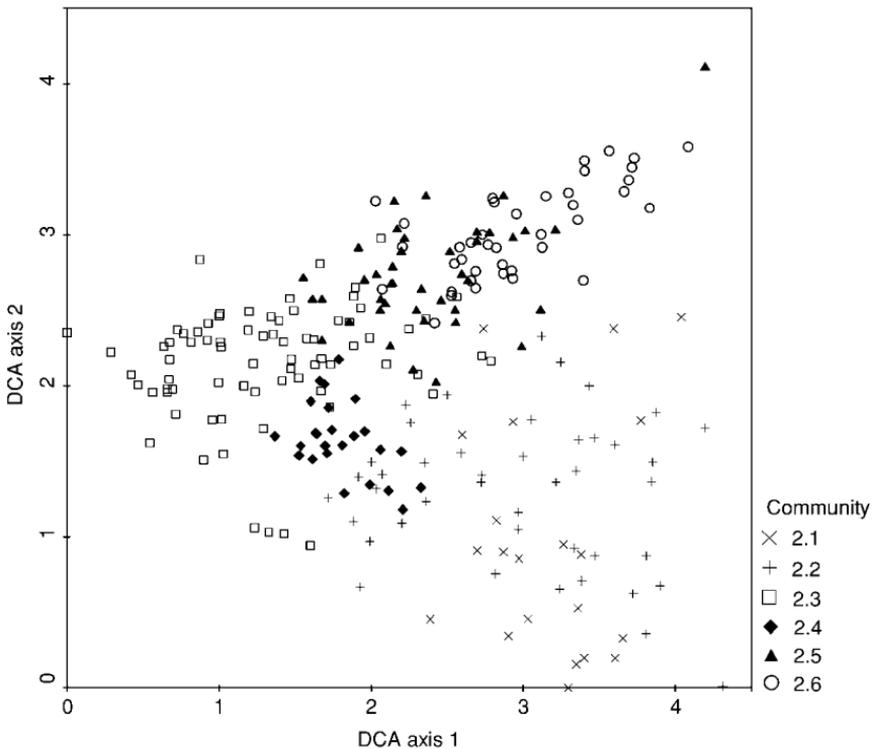


Fig. 5. Ordination diagram with axes 1 and 2 of a DCA revealing the floristic relationships between the Nordic *Alyso-Sedetalia* associations. 2.1: *Cladonio symphycaepae-Sedetum albi*, 2.2: *Ditricho flexicaulis-Sedetum acris*, 2.3: *Crepido pumilae-Allietum alvarensis*, 2.4: *Fulgensio bracteatae-Poetum alpinae*, 2.5: *Helianthemo oelandici-Galietum oelandici*, 2.6: *Gypsophilo fastigiatae-Globularietum vulgare* (Eigenvalues: axis 1: 0.478, axis 2: 0.432).

mostly represent the *Poo compressae-Saxifragetum tridactylitae* of anthropogenic sites.

The ordination diagram of the Nordic communities (Fig. 5) indicates a distinct floristic composition of the *Crepido-Allietum*, *Helianthemo-Galietum* and *Gypsophilo-Globularietum* from the mainland communities. The *Fulgensio-Poetum* is intermediate between the Ölandic and the mainland communities; the cluster is, however, still well separated. By contrast, the ordination diagram reveals no clear separation between the two mainland communities. This may be due to the high number of shared species, which often dominate the community, whereas character species are few and often have low degrees of cover.

When analysing the alvar communities separately (Fig. 6), except for the *Helianthemo-Galietum*, they form rather distinct clusters. The *Helianthemo-Galietum* is intermediate between the *Crepido-Allietum* and the *Gypsophilo-Globularietum*. The floristic gradient between

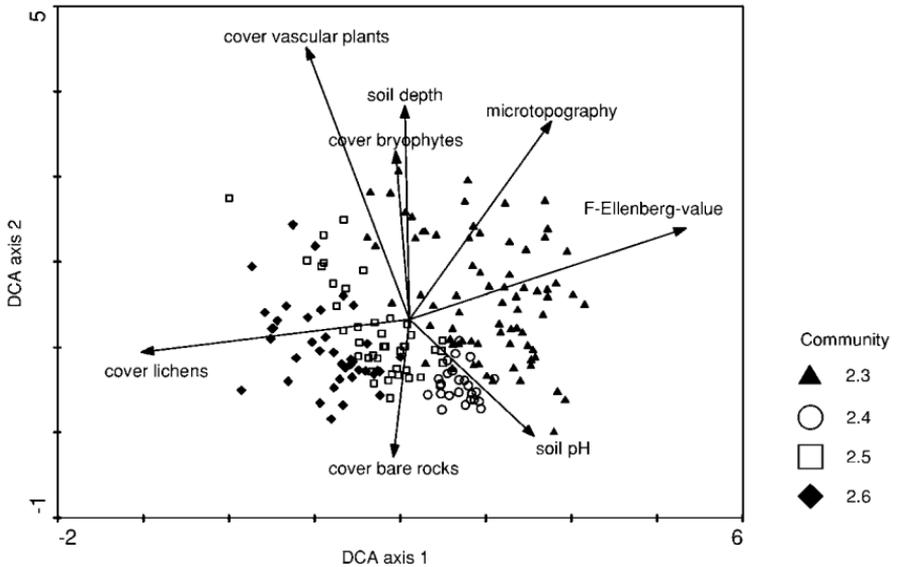


Fig. 6. Ordination diagram with axes 1 and 2 of a DCA revealing the floristic relationships between the Ölandic alvar associations (suballiance *Tortello rigentis*-*Helianthemion oelandici*). In addition, correlations of the DCA axes with important environmental and structural variables are indicated. 2.3: *Crepidopumilae*-*Allietum alvarensis*, 2.4: *Fulgensio bracteatae*-*Poetum alpinae*, 2.5: *Helianthemion oelandici*-*Galietum oelandici*, 2.6: *Gypsophila fastigiatae*-*Globularietum vulgaris* (Eigenvalues: axis 1:0.492, axis 2:0.352).

Table 2. Spearman Rank Correlation coefficients relating sample scores along extracted DCA axes to environmental and structural variables. The analysis was performed on the relevés of the Ölandic alvar communities. Important values ($r > |0.5|$) are indicated by bold type.

Eigenvalue	DCA axis 1	DCA axis 2
	0.49	0.35
Soil pH (H ₂ O)	0.382***	-0.371***
Soil depth (cm)	-0.045	0.463***
Microtopography (cm)	0.440***	0.255***
F-Ellenberg-value	0.510***	0.181*
Cover bare rocks (%)	-0.145	-0.382***
Cover vascular plants (%)	-0.254***	0.638***
Cover bryophytes (%)	-0.126	0.333***
Cover lichens (%)	-0.731***	-0.109

*** $p < 0.001$, * $p < 0.05$

these three communities is represented by the first ordination axis. The second axis mainly separates the *Fulgensio*-*Poetum* from the other communities.

Table 2 gives the correlation coefficients between the relevé scores on the DCA axes and environmental and vegetation structure variables. The first ordination axis mainly represents a gradient in soil moisture, whilst the second mainly corresponds to a gradient in soil depth. Soil pH is negatively correlated with axis two, which may be due to the humus content increasing with soil depth, which results in lower soil pH values. Microtopography was positively correlated with the first two axes. The cover of vascular plants and of bryophytes is positively correlated with axis two. The cover of lichens is negatively correlated with the first axis since moist sites generally are poor in lichens.

4.4 Comparison of the environmental conditions and the vegetation structure of the Ölandic communities

Table 3 compares the site conditions and vegetation structure of the Ölandic alvar communities. As indicated by the ordination analysis (Fig. 6, see 0), the floristic differentiation between these can be explained mainly by differences in soil moisture and soil depth.

The *Crepido-Allietum* grows at the wettest sites, which are poorly drained and affected by frost action, which leads to polygon structures and to an often significant microtopography. The *Helianthemo-Galietum* grows in considerably drier places, which, however, are still regularly inundated in winter. By contrast, the *Gypsophilo-Globularietum* occurs on well-drained sites, especially in karst areas. Sites with this community often lie close to *Juniperus*-shrubs in a southern exposition, which leads to an especially warm microclimate. The sites of the *Fulgensio-Poetum* are ecologically clearly distinguished from the other communities by extremely shallow soils and a much higher coverage of bare rocks (mean 28.4%). The soil moisture and the impact of frost disturbances are intermediate and comparable to those of the *Helianthemo-Galietum*. All four associa-

Table 3. Structure and environmental conditions of the Ölandic alvar communities. Mean values and standard deviations (in brackets) are given. Homogeneous groups ($p < 0.05$) are indicated by superscript letters; 2.3: *Crepido pumilae-Allietum alvarensis*, 2.4: *Fulgensio bracteatae-Poetum alpinae*, 2.5: *Helianthemo oelandici-Galietum oelandici*, 2.6: *Gypsophilo fastigiatae-Globularietum vulgare*.

	2.3 <i>n</i> = 74	2.4 <i>n</i> = 25	2.5 <i>n</i> = 40	2.6 <i>n</i> = 38
Soil pH (H ₂ O)	7.4 (0.6) ^a	7.4 (0.4) ^a	7.4 (0.5) ^a	7.2 (0.5) ^a
Soil depth (cm)	7.1 (3.9) ^b	2.4 (1.3) ^a	5.7 (2.9) ^b	5.1 (2.9) ^b
Microtopography (cm)	5.2 (5.6) ^b	1.6 (2.1) ^a	0.5 (1.5) ^a	0.3 (1.2) ^a
F-Ellenberg-value	4.5 (0.9) ^b	3.3 (0.7) ^a	3.6 (0.7) ^a	3.5 (0.5) ^a
Cover bare rocks (%)	3.9 (10.5) ^a	28.4 (26.5) ^b	4.6 (6.7) ^a	8.1 (10.6) ^a
Cover vascular plants (%)	56.9 (19.5) ^b	18.3 (12.9) ^a	50.7 (16.6) ^b	59.6 (13.1) ^b
Cover bryophytes (%)	26.3 (21.3) ^a	24.5 (15.2) ^a	18.7 (13.3) ^a	26.6 (17.0) ^a
Cover lichens (%)	5.2 (6.5) ^a	10.2 (11.0) ^a	20.6 (14.8) ^b	25.2 (13.6) ^b

tions inhabit equally base-rich soils, with pH values mostly above the neutral point.

With decreasing soil depth, the cover of vascular plants decreases: With a mean cover of 18.4 %, the field layer of the Fulgensio-Poetum is much more poorly developed than that of the other communities with a mean cover of about 50 %. Bryophyte cover is high in all communities. Lichen cover, by contrast, increases with decreasing soil moisture; both the Helianthemo-Galietum (14.8 %) and the Gypsophilo-Globularietum (13.6 %) show a considerable cover of mainly fruticose lichens. By contrast, the lichen layer of the Fulgensio-Poetum is dominated by crustose lichens.

4.5 Differences in species diversity among communities

The species density of the Nordic Alysso-Sedetalia communities proved to be distinctly higher than that of their Central European counterparts, with an average of 36.0 species per 4 m² relevé in the least diverse Nordic community compared to 17.7 species on 4 m² in Central Europe (Table 4). This trend also holds true when the species numbers of vascular plants, bryophytes and lichens are considered separately. Likewise, the picture remains essentially the same when excluding the Central European relevés of the Poo compressae-Saxifragetum tridactylitae of heavily anthropogenic sites.

Comparing Nordic communities of the Ölandic alvar areas (2.3–2.6) with those from non-alvar sites on the Swedish mainland and in Norway (2.1, 2.2), the bryophyte species richness of the alvar communities is significantly higher (F -test, $p < 0.001$). The same is true for lichen species richness, except for the Crepido-Allietum. By contrast, the vascular plant species richness of the Ölandic communities as a whole is significantly lower (F -test, $p = 0.010$).

Table 4. Total and group specific species densities of the Nordic Alysso-Sedetalia associations on 4 m² (mean values, standard deviations in brackets). For comparison, the values for the Central European alliance are also shown. Homogeneous groups ($p < 0.05$) are indicated by superscript letters. All. 1: Alysso-Sedion (= Central European relevés), 2.1: Cladonio symphycaepae-Sedetum albi, 2.2: Ditricho flexicaulis-Sedetum acris, 2.3: Crepido pumilae-Allietum alvarensis, 2.4: Fulgensio bracteatae-Poetum alpinae, 2.5: Helianthemo oelandici-Galietum oelandici, 2.6: Gypsophilo fastigiatae-Globularietum vulgare.

	All. 1 <i>n</i> = 35	2.1 <i>n</i> = 6	2.2 <i>n</i> = 14	2.3 <i>n</i> = 74	2.4 <i>n</i> = 25	2.5 <i>n</i> = 41	2.6 <i>n</i> = 39
Total species number	17.7 (6.9) ^a	36.0 (12.9) ^b	41.4 (9.7) ^b	42.5 (14.5) ^b	48.4 (12.0) ^{bc}	52.9 (10.8) ^c	53.6 (12.6) ^c
Vascular plants	13.9 (4.9) ^a	23.3 (4.6) ^{bc}	22.3 (4.6) ^{bc}	19.2 (8.2) ^b	12.1 (6.1) ^a	20.5 (6.2) ^{bc}	23.2 (4.3) ^c
Bryophytes	2.5 (2.3) ^a	7.2 (6.4) ^b	9.8 (3.5) ^b	17.7 (7.8) ^c	22.7 (7.0) ^c	19.3 (7.6) ^c	18.8 (8.7) ^c
Lichens	1.3 (1.4) ^a	5.3 (2.9) ^b	9.2 (5.7) ^{bc}	5.1 (3.9) ^b	13.0 (4.6) ^d	12.9 (4.5) ^d	11.5 (5.2) ^{cd}

The Gypsophilo-Globularietum is the community richest in species, with a mean species density of 53.6 species per 4 m² plot; the most diverse relevé has 80 species. The lowest species densities within the alvar communities are found in the Crepido-Allietum with a mean of 42.5 species. The variation in species numbers, however, is extremely high. Species densities on 4 m² extend from 9 species at sites most heavily influenced by frost action and inundation to 72 species on places with deeper, more stable soils.

For all the Ölandic alvar communities, species numbers of bryophytes and lichens exceeds the number of vascular plants (Table 4). By contrast, cryptogams in the Central European relevés are of minor importance for species diversity and community structure. In the Fulgensio-Poetum, cryptogams provide more than 70% of all species. The lowest number of cryptogams is observed in the Crepido-Allietum, with especially low numbers of lichen species (5.1 species).

Vascular plant species richness decreases from the Gypsophilo-Globularietum with a mean of 23.2 species, through the Helianthemo-Galietum with 20.5 species and the Crepido-Allietum with 19.5 species, to the Fulgensio-Poetum with only 12.1 species.

5 Discussion and conclusions

5.1 Effects of the relevé properties

The sharp distinction between Central European and Nordic Alysso-Setetalia relevés both in terms of species composition (Table 1) and species densities (Table 4) may be partly caused by different data quality, i.e. the less complete recordings of cryptogams by Central European authors. However, since even relevés from authors known to treat cryptogams very accurately show this difference, this seems to be a real effect. When carrying out an ordination analysis just with the vascular plant taxa, we also obtained the same clear separation between the Northern and the Central European communities.

Within the Nordic relevés, one major problem could be the strong geographic bias of the data available from outside Öland. This may have led to the misinterpretation of some species as diagnostic whose high presence degree is in reality due to regional effects (autocorrelations). Relevés more evenly distributed over the southern part of Northern Europe would thus be desirable in the future. This may result in less sharp delimitations of our syntaxa, but since they now have large numbers of diagnostic species, they should nonetheless prove to be valid in essence.

5.2 Syntaxonomy

5.2.1 Placing the results into a taxonomic classification scheme (Table 5)

Dry grassland communities of shallow, skeletal soils as a whole have been treated on different phytosociological levels by various authors (e.g. KOR-

Table 5. Overview of the syntaxa treated in this paper. An asterisk (*) indicates syntaxa that are newly named or described in Appendix 1. The sources for all author citations are included in the reference list.

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- Class: **Koelerio-Corynephoretea** Klika in Klika & Novák 1941 – Dry grasslands of sandy and shallow, skeletal soils
- Subclass A: **Koelerio-Corynephorenea** (Klika in Klika & Novák 1941) Dengler in Dengler et al. 2003 – Dry grasslands of sandy soils
- Subclass B: **Sedo-Scleranthenea** (Br.-Bl. 1955) Dengler in Dengler et al. 2003 – Dry grasslands of shallow, skeletal soils
- Order I: **Sedo-Scleranthetalia** Br.-Bl. 1955 – Acidophilous dry grasslands of shallow, skeletal soils
- Order II: **Alysso alyssoidis-Sedetalia** Moravec 1967 – Basiphilous dry grasslands of shallow, skeletal soils
- All. 1: **Alysso alyssoidis-Sedion** Oberd. & T. Müller in T. Müller 1961 – Temperate zone
- All. 2: **Tortello tortuosae-Sedion albi** Hallberg ex Dengler & Löbel 2006* – Hemiboreal zone
- Suball. 2a: **Tortello tortuosae-Sedenion albi** (Hallberg ex Dengler & Löbel 2006*) Dengler & Löbel 2006* – Non-alvar sites
- Ass. 2.1: **Cladonio symphycaepae-Sedetum albi** Tx. 1951 nom. invers. propos.
- Ass. 2.2: **Ditricho flexicaulis-Sedetum acris** Hallberg 1971
- Suball. 2b: **Tortello rigentis-Helianthemenion oelandici** suball. nov. Dengler & Löbel 2006* – Alvar sites
- Ass. 2.3: **Crepido pumilae-Allietum alvarensis** Krahulec et al. ex Dengler & Löbel 2006*
- Ass. 2.4: **Fulgensio bracteatae-Poetum alpinae** (Albertson 1950) Dengler & Löbel 2006*
- Ass. 2.5: **Helianthemo oelandici-Galietum oelandici** Krahulec et al. ex Dengler & Löbel 2006*
- Ass. 2.6: **Gypsophilo fastigiatae-Globularietum vulgaris** Krahulec et al. ex Dengler & Löbel 2006*
-

NECK 1978, JULVE 1993, MUCINA & KOLBEK 1993, POTT 1995, DIERSSEN 1996, SCHAMINÉE et al. 1996b, SCHUBERT et al. 2001, RIVAS-MARTÍNEZ 2002). From order-level upwards, we follow the suggestions of DENGLER (2001, 2003: 201, in DENGLER et al. 2003, 2004) who regards them as a subclass within a broadly conceived class *Koelerio-Corynephoretea* and subdivides them into an acidophytic order *Sedo-Scleranthetalia* s. str. and a basiphytic order *Alysso-Sedetalia*.

Both cluster analyses and ordinations (see 4.2, 4.3) revealed a clear separation of the Nordic and Central European relevés of the *Alysso-Sedetalia*. It is therefore justified to treat them as two different alliances. We found that the Central European alliance (*Alysso-Sedion* s. str.) is characterised mainly negatively, whereas the Nordic alliance (*Tortello tortuosae-Sedion albi* all. nov., see Table 5) has many character- and differential taxa (Table 1). Moreover, the potential character species of the *Alysso-Sedion* only attain low presence degrees. The 27% listed for *Arenaria*

serpyllifolia ssp. *leptocladus* may even be too high since many records of this taxon in Central European relevés are erroneous (BAMMERT 2004). Species such as *Sedum sexangulare*, *Medicago minima* and *Alyssum alyssoides* (see Table 1) can only be accepted as differential species of the Alyso-Sedion since they have similar or even higher presence degrees in other alliances of the Koelerio-Corynepherea or Festuco-Brometea Br.-Bl. & Tx. ex Kika & Hadač 1944 (Dengler unpubl.).

The Nordic alliance Tortello-Sedion is characterised by the cryptogams *Cladonia pocillum*, *Distichum capillaceum*, *Ditrichum flexicaule* and *Encalypta rhabtocarpa* (Table 1), which are all also indigenous in Central Europe but are obviously much rarer in the Alyso-Sedion. The numerous differential taxa (see Table 1) of the Tortello-Sedion belong to very different ecological, sociological and chorological groups, of which arctic-alpine taxa (*Cetraria islandica*, *Poa alpina*), "mesophilous" taxa (e.g. *Galium verum*, *Medicago lupulina*, *Plantago lanceolata*), acidophilous taxa (e.g. *Cetraria aculeata*) and species indicating temporarily moist soils (*Prunella vulgaris*, *Sagina nodosa*) can be highlighted. Within the Nordic communities, those from alvar regions are floristically very distinct, as already shown by DIERSSEN (1996: Table 84; also see 4.2 and Fig. 5). We have been able to add several further character and differential taxa to those mentioned by him (see Table 1). We therefore treat the four alvar associations as a separate suballiance (Tortello rigentis-Helianthemion oelandici, see Table 5). Its character taxa comprise on the one hand bryophytes and lichens with a wide geographic distribution, which are, however, much rarer in other vegetation types and in Alyso-Sedetalia communities of other regions, and on the other hand taxa with restricted distribution areas. Of these, *Helianthemum oelandicum* ssp. *oelandicum* is endemic to Öland, and *Allium schoenoprasum* var. *alvarense*, *Festuca oelandica*, *Hieracium ×dichotomum* and *Silene uniflora* ssp. *petraea* are only known from Öland and Gotland (MOSSBERG & STENBERG 2003, JONSELL & KARLSSON 2004). *Arenaria gothica*, as a further probable character species of the suballiance (cf. ALBERTSON 1946), only occurs in the alvar areas of Gotland and Kinnekulle (Västergötland) but not on Öland. *Tortella rigens*, described by ALBERTSON (1946), is the sole endemic cryptogam species. It is quite common in the alvar areas of Öland, Gotland and Kinnekulle, but records from non-alvar areas in Sweden are very rare, and outside of Sweden this species is only known from Estonia (ALBERTSON 1946, NYHOLM 1989).

The six Nordic associations of the Alyso-Sedetalia proved to be floristically well defined, and the classification of the Ölandic communities is even supported by an indirect ordination analysis whose axes clearly represent a gradient in abiotic site conditions (Fig. 6). The character species of the associations of the Tortello-Helianthemion comprise two further Öland endemics: *Crepis tectorum* ssp. *pumila* and *Galium oelandicum* (JONSELL & KARLSSON 2004). The occurrences of the other characteristic vascular plants in the Nordic alvar regions are geographically separated outliers from their main distribution areas in southwest Europe (*Globularia vulgaris*, *Sisymbrium supinum*), southeast Europe (*Gypsophila fastigiata*)

and central Asia (*Artemisia rupestris*; e.g. HULTÉN & FRIES 1986). According to the concept of BERGMIEER et al. (1990) and DENGLER (2003), they can nevertheless be regarded as character species of Nordic associations if the Tortello-Helianthemion is nowhere sympatric with the superior syntaxon of the communities in which these species are characteristic in their main distribution range.

We found both positively and (mainly) negatively characterised syntaxa at all the taxonomic levels that were treated: Of the two discerned Alysso-Sedetalia alliances, the Central European Alysso-Sedion does not have any frequent character species of its own, and is thus regarded as the central alliance of the order. Within the Nordic countries, the stands outside the alvar regions in fact share the character species of the alliance Tortello-Sedion with those from the alvar areas, but have only few differential and no character species of their own. These two associations are therefore regarded as the central suballiance Tortello tortuosae-Sedion albi (see Table 5) opposed to the positively characterised Tortello-Helianthemion of the alvars. Within each of these suballiances, there is one central association, namely the Cladonio symphycaepae-Sedetum albi (see 0) and the Helianthemo oelandici-Galietum oelandici (see 0).

5.2.2 Comparison of the proposed taxonomic scheme with other classifications

Early classification attempts often regarded the basiphilous dry grassland communities of shallow, skeletal soils in Northern Europe as belonging to the class Festuco-Brometea (e.g. ALBERTSON 1946). BRAUN-BLANQUET (1963) described the Helianthemo-Globularion which comprises alvar communities rich in *Globularia vulgaris*. According to him, this should be endemic to Öland, Gotland and Estonia and should be placed in the continental order Festucetalia valesiaceae Br.-Bl. & Tx. ex Br.-Bl. 1950 of this class. He only subordinated very open moss-rich stands ("*Schistidium apocarpum*-*Sedum album*-Initiale") to the Sedo-Scleranthion Br.-Bl. 1955. BRAUN-BLANQUET's work, however, is problematic since his relevés did not conform to the homogeneity criterion and comprised a mosaic of dry grassland communities of shallow, skeletal soils and such of more profound soils (e.g. KRAHULEC et al. 1986, DENGLER et al. 2003), which had already been separated as "Festucetum" vs. "Avenetum" by ALBERTSON (1946, 1950). Nevertheless, ROYER (1991) in his global synthesis of the Festuco-Brometea took up BRAUN-BLANQUET's concept of the Helianthemo-Globularion, and has recently been followed by RODWELL et al. (2002). Today, however, most authors agree that the vegetation types treated in our study belong as a whole to the dry grassland communities of shallow, skeletal soils (Alysso-Sedetalia or Sedo-Scleranthetalia) within the class Koelerio-Coryneporetea (Sedo-Scleranthetea), and only the "Avenetum" of ALBERTSON (1946, 1950) should be included in the Festuco-Brometea (e.g. HALLBERG 1971, KRAHULEC et al. 1986, DIERSSEN

1996). This is supported by the numerical analyses of BENGTTSSON et al. (1988) and our own data (cf. LÖBEL 2002).

HALLBERG (1971) proposed a separate alliance Tortello-Sedion, comprising the Scandinavian dry grassland communities of shallow, skeletal soils over base-rich bedrock. He stated that the ground layer of these communities is much better developed than that of the Central European stands of the Alysso-Sedion, which is confirmed by our findings (see 5.2).

Regarding the communities outside the alvar areas (Tortello-Sedion), we were able to distinguish two associations. The relevés of HALLBERG (1971) as a whole hold a quite distinct position in our classification. However, his "Sedo-Tortelletum", *Ditricho-Sedetum* and *Arenaria serpyllifolia-Sedum acre* community, could not be accepted at the rank of associations because of the lack of character species of their own. All other relevés from Northern Europe outside the alvar regions, which have been published under different names (see Appendix 1), have to be placed in the somewhat heterogeneous central association Cladonio-Sedetum according to the principles pointed out in section 3.5.1.

KRAHULEC et al. (1986) suggested an endemic alliance Helianthemo-Cetrarion within the Sedo-Scleranthetea (Koelerio-Corynephoretea) which should include the Helianthemo-Galietum (2.5) and the Gypsophilo-Globularietum (2.6), whereas according to them the Crepido-Allietum (2.3) should belong to the Alysso-Sedion. In his synthesis, DIERSSEN (1996) accepted the three named associations but included all of them in the Alysso-Sedion. As shown by our ordination analyses, the Crepido-Allietum is floristically more closely related to the Helianthemo-Galietum than to the communities of the Scandinavian mainland and Central Europe (see Fig. 5). Therefore, a separation of the alvar communities into different alliances does not appear to be justified.

The delimitation of the alvar communities on Öland has been less controversially discussed than their syntaxonomic position. Already ALBERTSON'S (1950) communities more or less correspond to our units (see Appendix 1). The associations provisionally established by KRAHULEC et al. (1986) are even more similar to ours, which is why we took up their names. The sole exception is the differentiation of the Fulgensio-Poetum from the Crepido-Allietum. Whereas our data suggest a clear floristic and ecological distinction between these communities (see Table 1), KRAHULEC et al. (1986) could not differentiate between them on the association level. This was probably due to the low number of their relevés and the fact that they excluded open moss and *Sedum* communities from their study. The Fulgensio-Poetum was more clearly separated in the subsequent study of BENGTTSSON et al. (1988); their cluster 6 largely corresponds to our association.

5.2.3 Methodological issues

Two aspects of the classification methodology will be discussed here: (1) How to deal adequately with plant communities which are as rich in cryp-

togams as the Alysso-Sedetalia? (2) How far do the established character species and thus the classification results depend on context?

(1) In our study, we focussed on holocoenoses and thus included – as far as possible – all vascular plants and macroscopically visible non-vascular plants in our relevés. Although we only analysed stands with a herbaceous layer, the cryptogam layer often exceeded it in terms of coverage or even of above-ground phytomass. In addition, the species richness of bryophytes and lichens combined was in most cases higher than that of vascular plants (see Table 4). Given the great importance of non-vascular plants within the studied communities and their very distinctive distribution patterns among these (see Table 1), it seems reasonable to use bryophytes and lichens as diagnostic species as well. Epilithic and epiphytic species should preferably also be included in the classification (DENGLER 2003) since they form characteristic parts of certain communities and may have a highly distinctive value (WILMANN & BIBINGER 1968, SCHUHWERK 1986, DENGLER 2003). As non-epigeic cryptogams were not recorded in most of the included literature data, however, we had to refrain from using them as diagnostic in the present study. Some authors have stated that the cryptogam layer of a vegetation type should be analysed on a finer scale than the field layer since the “minimal area” of the former would be much smaller (e.g. BARKMAN 1968, DIERSCHKE 1994). However, the concept of “minimal areas”, suggesting that species-area curves would show a saturation level at a certain point of the spatial scale, is a mere delusion engendered by the inappropriate linear plotting of this essentially non-linear relationship. In fact, both theoretical considerations (e.g. WILLIAMSON et al. 2001, DENGLER 2003) and the appropriate analysis (i.e. with logarithmic transformation of the axes) of a large body of empirical data (e.g. HOPKINS 1955, 1957, KILBURN 1966, KAMMER 1997, DOLNIK 2003, DENGLER 2005) show that every increase in plot size will result in an increase in the mean species richness. In the case of the Nordic Alysso-Sedetalia communities, the separate species-area curves for vascular plants, bryophytes and lichens in the log-log space show a rather similar shape and run nearly parallel (Öland, 1 cm²–9 m²: LÖBEL 2002, LÖBEL et al. 2004; Estonia, 1 cm²–100 m²: BOCH & DENGLER unpubl.). In addition to the study of the holocoenoses, the analysis of the different societies (merocoenoses) that form them would have been an interesting aspect but was beyond the scope of this paper. These two approaches to study vegetation are complementary rather than mutually exclusive but should be kept clearly apart as regards their terminology (DU RIETZ 1966, BARKMAN 1968, 1973, WILMANN 1970, DENGLER 2003). There have been attempts to classify holocoenoses not based on the taxa that occur but on their constituent synusiae (merocoena), either for the non-epigeic synusiae alone (e.g. SCHUHWERK 1986, HOBBOHM 1998) or for all of them (“integrated synusial approach”; e.g. GILLET & GALLANDAT 1996). Such an approach, however, seems inappropriate for syntaxonomy, i.e. the establishment of a hierarchical system of holocoena, since it has a number of shortcomings, and so it was not followed here: (1) Before this approach can reasonably be applied, a well-founded and com-

plete synusial system must be available. At present, however, only rather inconsistent systems are available for cryptogamic synusiae (because in almost any recent overview they are confounded with one-layered holocoena) and practically none for the synusiae of vascular plants. (2) Even if such synusial systems were available, the data collection would be a much more time-consuming task since before the first relevé of a phytocoenosis proper could be made a comprehensive study (relevés, classification) of all the synusiae present would have to be carried out. (3) Though the expenditure would be greater, the results would be less objective and less precise since (i) both the classification of synusiae and their delimitation on the terrain involve many additional subjective decisions, and (ii) the resulting vegetation tables nevertheless fail to give complete species data (composition, richness) for the plots of the holocoenoses. Finally, one may ask whether the communities studied, especially the Fulgensio-Poetum, belong to the herbaceous vegetation at all. Similar vegetation types have indeed been included in mere cryptogamic communities of the alliance *Toninion caeruleonigricantis* Hadač 1948 by other authors (e.g. GAUCKLER 1957, BORNKAMM 1958). As their stands also include a considerable proportion of vascular plants, it seems questionable why they should be regarded as belonging to the one-layered cryptogam vegetation. Since BORNKAMM's stands rarely exceed 0.1 m² in size, it also seems doubtful whether these belong to an "independent" association, as he claims, rather than forming a special synusia that constitutes an integrative part of the dry grassland community, in the gaps between whose tussocks it grows. Since we do not know of any methodological proposal for the *a priori* delimitation of herbaceous against cryptogam communities, we have had to apply a new definition (see 3.5.1), which, of course, is open to criticism. Further studies are needed to test whether this proposal is appropriate and whether such a classificatory separation of herbaceous and cryptogam communities on structural grounds (BERGMEIER et al. 1990, DIERSCHKE 1992, DENGLER 2003) is necessary at all. It may prove to be superfluous when the mosses and lichens (nearly) always occur together with vascular plants, since the really independent (e.g. epilithic) cryptogam communities can be discerned by their floristic composition alone without additional structural criteria.

(2) Diagnostic species and thus syntaxonomic classifications largely depend on context, i.e. which vegetation types and from which area are included in the analysis (BRUELHEIDE & CHYTRÝ 2000, CHYTRÝ et al. 2002, DENGLER 2003). The aim of syntaxonomy should be to work towards a single worldwide system of all syntaxa since, according to the ICPN, at least formalised syntaxon names are not applicable for multiple systems (compare DENGLER 2003). Even with the largest available vegetation data-banks, we are far from this goal (CHYTRÝ et al. 2002). Using information complementary to the data stored in the relevés and included in the numerical analyses, such as synoptic tables and species lists from other regions and syntaxa or chorological data, it is, however, possible to approach a great deal closer to this goal. So we only assigned the character species status to a taxon when it fulfilled the relevant criteria within our data set

and we had no indication that it is present to a similar or higher degree in other syntaxa not included in our study. In addition to the availability of data, methodological principles also set the “context” of a classification. We have used the term “character species” not in an absolute manner but with (i) structural and (ii) implicit geographical limits (see 3.5.1; BERGMIEER et al. 1990, DIERSCHKE 1992, DENGLER 2003). We were therefore able to (i) regard cryptogam taxa as character species of a herbaceous vegetation type without knowing how frequently they occur in pure cryptogam communities, and (ii) accept taxa with a widely disjunct occurrence as character species of Nordic Alysso-Sedetalia communities regardless of whether they are character species of other syntaxa in their major distribution range, an information that is hardly available (see 3.5.1). Accepting this methodological proposal thus reduces the context sensitivity of a classification and enhances the stability of its results.

5.3 Synchorology

The synchorological map of DENGLER (2003: 218) shows that the subclass Sedo-Scleranthenea has two major distribution ranges, (i) the mountainous regions of Central and Western Europe including the adjacent high mountains of Southern Europe, and (ii) the southern parts of Norway, Sweden and Finland plus Estonia. These “cores” clearly correspond to the two alliances worked out in this paper, Alysso-Sedion and Tortello-Sedion, respectively. They are separated by a wide “gap” in the North Central European Lowlands, where dry grassland communities of shallow, skeletal soils are only represented by the *Poo compressae-Saxifragetum tridactylitae* on anthropogenic substrata (cf. DENGLER 2004). This geographic disjunction possibly enhanced the floristic distinction between the two alliances.

In the following section, we will try to give an outline of the overall distribution of the Tortello-Sedion associations (the major regions referred to are indicated in the map, Fig. 1), based both on the relevés included in this study and on other data such as relevés not in accordance with our criteria (see 3.3), species lists and verbal descriptions.

The *Cladonio-Sedetum* as central association of the suballiance Tortello-Sedion is probably the most widely distributed association and we expect it to occur throughout the southern part of Northern Europe and to reach the furthest northwards of the six communities. We found additional records from the Oslofjord (HALVORSEN 1980: blocks I–III) and the Trondheimfjord in Norway (FREMSTAD 1997: units F3a and F3b) as well as from the Swedish provinces of Uppland (ALMQUIST 1929: “Succulent- och terofytsamhällen”) and Västergötland (ALBERTSON 1946: “Sedetum tortellosum” p. min. p.). Recently, stands that belong to the *Cladonio-Sedetum* have been reported from gravel deposits near the seashore on the Estonian island of Saaremaa (cf. BOCH & DENGLER 2004). Few indications of phytocoenoses similar to the *Ditricho-Sedetum* of Bohuslän were available from other regions; however, we consider it possi-

ble that this association occurs on shell deposits all along the coasts of southern Norway and Sweden. For example, HALVORSEN (1980: blocks IV and V) recorded a very similar species combination, even including the supposed character species *Tortella fragilis*, from a small island in the Oslofjord. A species list by PETERSSON (1958: Table 31) from a Litorina shore ridge on Gotland also shows some similarities with this community, including *Bacidia bagliettoana*.

By contrast, the second suballiance, Tortello-Helianthemenion, seems to be restricted to the "real" alvar areas, i.e. Öland, Gotland, Västergötland (Kinnekulle) and Estonia (west coast and Baltic islands). Though the character species of the four associations are partly absent from the alvar regions outside Öland, the phytocoenoses from there may be classified by the differential species that occur. In this wider delimitation, neither the Crepido-Allietum nor the Helianthemo-Galietum is endemic to Öland, as was supposed by KRAHULEC et al. (1986). As we understand it, both ALBERTSON's (1946) periodically inundated "*Festuca-Tortella-Schistidium*-subassociation" of his "*Festucetum tortellosum*" from Västergötland and alvar communities rich in *Artemisia rupestris* from Estonia, growing on sites heavily affected by frost movement (PÄRTEL et al. 1999, BOCH & DENGLER 2004), belong to the Crepido-Allietum. In addition to southern Öland, the Fulgensio-Poetum also occurs in a small alvar region on the northwest coast of this island (own observations), in Västergötland (ALBERTSON 1946) and on Gotland (DU RIETZ 1925, PETERSSON 1958, OTT et al. 1996). In a broadly conceived central association Helianthemo-Galietum, relevés from Västergötland (ALBERTSON 1946: "*Festuca-Tortella-Cetraria islandica*-subassociation" of the "*Festucetum tortellosum*" p. max. p.) may be subordinated alongside those from Öland and Gotland included in this study. Finally, the Gypsophilo-Globularietum is the geographically most delimited association which seems to be restricted to Öland, Stora Karlsö and Gotland (cf. PETERSSON 1958: Tables 19 and 28).

5.4 Phytodiversity

The Nordic dry grassland communities of shallow, skeletal soils have proved to be twice to three times as rich in species as their Central European counterparts (Table 4). With up to 80 species on 4 m², the Gypsophilo-Globularietum is even one of the plant communities with the highest species densities on a small scale documented so far (cf. DENGLER 2005). Only lichen-rich dwarf-shrub communities in Greenland (e.g. LÜNTERBUSCH & DANIÉLS 2004: up to 83 species on 4 m²) and meadow steppes in Russia (e.g. DONIȚĂ et al. 2003: up to 80 species on 1 m²) are known to have a similar or higher species richness on such plot sizes. What are the possible explanations for the extremely high small-scale species richness of these communities, especially those from the Great Alvar?

We suggest (1) a lower degree of competition, and (2) the smaller size of many plants, as possible reasons for the higher small-scale species densities

in different Nordic plant communities compared with their counterparts further south: (1) High interspecific competition in ecology is often regarded as reducing species densities (e.g. GRIME 1979, BEGON et al. 1990, GRACE 1999). In North European plant communities, competition should be lower than in Central European stands of the same type due – generally speaking – to a less productive environment (e.g. GOLDBERG & NOVOPLOANSKY 1997, PÄRTEL et al. 2000), i.e. a shorter vegetation period, a harsher climate and often less fertile soils. These less-competitive conditions also enable lichens and bryophytes to play a greater role in Nordic areas compared to similar temperate phytocoenoses. (2) Since these cryptogams are generally smaller than vascular plants, and individuals of vascular plant species in Nordic countries often do not reach the same size, as they do further south the higher small-scale species richness of many Nordic plant communities may be partly a “sampling effect”, i.e. the smaller the individuals, the more species can potentially co-occur in the same space (e.g. GOTELLI & COLWELL 2001).

As regards the outstanding species densities of the Tortello-Sedion, additional reasons must be considered. Many species of the Nordic dry grassland communities of shallow, skeletal soils, especially those of the alvar regions, occur as outliers or at the limit of their geographic ranges (e.g. STERNER & LUNDQVIST 1986, BENGTTSSON et al. 1988). The disjunct occurrences of southern European species are probably relicts from post-glacial warm periods favoured by the dry and warm summers. Arctic-alpine species on the other hand may be glacial relicts which survived in the Alyso-Sedetalia communities due to the harsh tundra-like winter conditions (e.g. ROSÉN 1982, STERNER & LUNDQVIST 1986, ROSÉN & BORGEGÅRD 1999). These species may have been accumulated in alvar areas (or may have evolved there even further) due to the often long-lasting land-use history, and now they form a large regional species pool. For the Great Alvar of Öland, KÖNIGSSON (1968) showed that it was extensively opened up by man from the beginning of the Bronze Age, i.e. the sub-Boreal. However, even in the millennia before that and in later periods, when trees and shrubs were able to re-invade the area due to decreasing land-use intensity, the Great Alvar was probably never covered so densely and so entirely by forests that species of open xerothermic sites could not survive there (the “Map of the Natural Vegetation of Europe” suggests a mosaic of dry grasslands alternating with scrubs and ash-oak forests as actual climax vegetation; BOHN & NEUHÄUSL 2000, BOHN et al. 2000; also see ROSÉN 1982, ROSÉN & VAN DER MAAREL 2000). Many studies have demonstrated the positive effect of regional species pool size on species density (e.g. PÄRTEL et al. 1996, PÄRTEL & ZOBEL 1999, DUPRÉ et al. 2002). Finally, the special environmental conditions of open alvar areas must also be taken into account as possible reasons for the extraordinarily high species densities. These sites show an extreme temporal variability between water logging and even inundation in winter and severe drought in summer. Since these contrasting environmental conditions regularly alternate, species adapted to both can co-exist. Moreover, a marked microtopography in some sites in-

creases the small-scale spatial heterogeneity, and we found that this is positively correlated with species density (LÖBEL et al. 2006).

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Appendix

Appendix 1. Nomenclatural overview of the syntaxa treated, including the necessary new descriptions and typifications as well as major synonyms. When there are nomenclatural problems, they are briefly outlined under “Note”. The sources for all the author citations are included in the reference list.

Tortello tortuosae-Sedion albi Hallberg ex Dengler & Löbel all. nov. hoc loco

Protologue: For diagnostic species, see Table 1.

Type: Ditricho-Sedetum Hallberg 1971: 69 [holotypus hoc loco]

Syn.: Festucion alvarens Albertson 1950 [Art. 3b, 34a], Helianthemo-Globularion Br.-Bl. 1963 nom. dub. p. p. [Art. 38; type: Phleo phleoidis-Veronicetum spicatae Br.-Bl. 1963 nom. dub. – holotypus], Anthyllido-Artemision campestris Sunding in Marker 1969 p. p. [Art. 3b], Tortello-Sedion Hallberg 1971 [Art. 3b], Helianthemo-Cetrarion (Br.-Bl. 1963) Krahulec et al. 1986 [Art. 8 resp. 29a; 10b]

Note: The Helianthemo-Cetrarion published by KRAHULEC et al. (1986) to replace the Helianthemo-Globularion of BRAUN-BLANQUET (1963) is not a valid name. It could only have been so if its authors had considered BRAUN-BLANQUET’s name as a *nomen dubium*. In this case, however, they would have been obliged to found their name on a new type (ICPN Art. 39 Sect. 2), which they failed to do since they were establishing their associations only provisionally.

Tortello tortuosae-Sedenion albi (Hallberg ex Dengler & Löbel all. nov.) suball. nov. Dengler & Löbel hoc loco

Protologue: For diagnostic species, see Table 1.

Basionym: Tortello tortuosae-Sedion albi Hallberg ex Dengler & Löbel (see above)

Type: Ditricho-Sedetum Hallberg 1971: 69 [holotypus (Art. 27a)]

Ass. 2.1: Cladonio symphycaepae-Sedetum albi Tx. 1951 nom. invers. propos.

Protologue: "*Sedum album-Cladonia symphycaepia*-Ass. (Albertson 1946)" (TÜXEN 1951: 166) (orthographically corrected: Sedo albi-Cladonietum symphycaepae Tx. 1951 [Art. 10b])

Type: Rel. A of Appendix 2 [neotypus hoc loco]

Syn.: Poo alpinae-Anthyllidetum ["Anthyllisetum"] vulnerariae Marker 1969 p. p. [syntax. syn.; type: MARKER (1969: Table 4, rel. 36) – lectotypus hoc loco], Sedetum acris Marker 1969 [syntax. syn.; type: MARKER (1969: Table 3, rel. 65) – lectotypus hoc loco]

Note: Since TÜXEN (1951: 168) did not state which of the associations in ALBERTSON (1946) should be replaced by his *nomen novum*, the Sedo albi-Cladonietum symphycaepae must be regarded as a new association. An author citation of "Albertson 1946" in brackets is therefore not correct. Furthermore, the epithet "*symphycaepia*" according to Santesson (1993) must be corrected to "*symphycaepa*" (ICPN Art. 41) and the inversion of the names must be proposed to the CNC (ICPN Art. 10b, 42).

Ass. 2.2: Ditricho flexicaulis-Sedetum acris Hallberg 1971

Protologue: "Ditricho-Sedetum" (HALLBERG 1971: 69)

Type: HALLBERG (1971: Table 14, rel. 15) [lectotypus hoc loco]

Syn.: Sedo-Tortelletum (Albertson 1946) Hallberg 1971 nom. amb. propos. p. p. [descr. incl., typo excl.; Art. 10b, 32a]

Note: For nomenclatural problems with the name Sedo-Tortelletum, see association 2.4.

Tortello rigentis-Helianthemion oelandici suball. nov. Dengler & Löbel hoc loco

Protologue: For diagnostic species, see Table 1.

Type: Helianthemo oelandici-Galietum oelandici Krahulec et al. ex Dengler & Löbel (see below) [holotypus hoc loco]

Syn.: Festuco-Globularienion vulgaris Royer 1991 p. max. p. [Art. 28a Sect. 2, 38; type: Phleo phleoidis-Veronicetum spicatae Br.-Bl. 1963 nom. dub. – holotypus]

Ass. 2.3: Crepido pumilae-Allietum alvarensis Krahulec et al. ex Dengler & Löbel ass. nov. hoc loco

Type: Rel. B of Appendix 2 [holotypus hoc loco]

Syn.: Festucetum alvarensis tortellosum Albertson 1950 p. p. [Art. 3e, 34a], Sedetum tortellosum Albertson 1950, non Albertson 1946 p. p. [typo excl.; Art. 3e, 31], Sedo albi-Tortelletum tortuosae Albertson 1950 nom. amb. propos. p. p. [typo excl.; Art. 10b], Crepido-Allietum alvarensis Krahulec et al. 1986 p. p. [Art. 3b, 34a]

Note: For nomenclatural problems with the name Sedo-Tortelletum, see association 2.4.

Ass. 2.4: Fulgensio bracteatae-Poetum alpinae (Albertson 1950) Dengler & Löbel nom. nov. hoc loco

Basionym: Sedo albi-Tortelletum tortuosae Albertson 1950 nom. amb. propos. p. p. [typo incl.; Art. 10b]

Type: ALBERTSON (1950: Table 1, rel. 6) [lectotypus hoc loco]

Syn.: Sedetum tortellosum Albertson 1946 p. max. p. [Art. 3e], "*Sedum album-Tortella tortuosa-Cladonia symphycaepia*-association" Albertson 1946 [Art. 34c], Sedetum

tortellosum Albertson 1950 p. p. [typo incl.; Art. 3e, 31], Sedo-Tortelletum (Albertson 1946) Hallberg 1971 nom. amb. propos. p. p. [typo. incl., descr. excl.; Art. 10b, 32a; type: ALBERTSON (1946: Table 2, rel. 5) – lectotypus hoc loco], Crepido-Allietum alvarense Krahulec et al. 1986 p. p. [Art. 3b, 34a]

Note: The “Sedetum tortellosum” was originally described by ALBERTSON (1946: 45) from a little alvar area in Västergötland. He used this name as a short version for his “*Sedum album-Tortella tortuosa-Cladonia symphyrcarpia*-association”. However, both names are illegitimate according to the ICPN. In a subsequent work on the alvar vegetation of Öland, ALBERTSON (1950: 284) again used the name “Sedetum tortellosum”, but this time accompanied by “*Sedum album-Tortella tortuosa*-Ass.” as an alternative form. The latter is a legitimate name according to the ICPN but must be orthographically corrected to “Sedo albi-Tortelletum tortuosae” (ICPN Art. 41b). Furthermore, the name sequence ought to be reversed by a decision of the CNC (ICPN Art. 10b). Since ALBERTSON (1950) did not explicitly publish this name as a *nomen novum* for the illegitimate name in his earlier work, it must be considered as the description of a new syntaxon. Its type therefore must be selected from the relevés included in ALBERTSON (1950). The sociations subordinated to the Sedetum tortellosum in 1946 belong to a large extent to our association 2.4, whereas in 1950 only one sociation belongs here while the second resembles our association 2.3. The situation is further complicated by HALLBERG (1971: 64) who replaced the Sedetum tortellosum Albertson 1946 by the *nomen novum* Sedo-Tortelletum. He used this name for our association 2.2 (belonging to the other suballiance!) but because of his reference to ALBERTSON (1946) the type must be selected from the relevés published there, i.e. it belongs to our association 2.4. The names Sedetum tortellosum and Tortello-Sedetum have thus been used for at least three different associations in the present system, partly in accordance with their respective types, partly not. We are therefore applying to the CNC to reject the name Sedo (albi)-Tortelletum (tortuosae) with whatever author citation, as a *nomen ambiguum*.

Ass. 2.5: Helianthemo oelandici-Galietum oelandici Krahulec et al. ex Dengler & Löbel ass. nov. hoc loco

Type: Rel. C of Appendix 2 [holotypus hoc loco]

Syn.: Sedo-Cetrarietum islandicae Du Rietz 1925 [Art. 3d (Grundsatz II Abs. 2)], Festucetum tortellosum Albertson 1946 p. max. p. [Art. 3e], Festucetum alvarense cetrariosum Albertson 1950 [Art. 3e], Festucetum alvarense tortellosum Albertson 1950 p. p. [Art. 3e, 34a], Helianthemo-Galietum oelandici Krahulec et al. 1986 [Art. 3b]

Ass. 2.6: Gypsophilo fastigiatae-Globularietum vulgaris Krahulec et al. ex Dengler & Löbel ass. nov. hoc loco

Type: Rel. D of Appendix 2 [holotypus hoc loco]

Syn.: Avenetum alvarense Albertson 1950 p. p. [Art. 34a], Phleo phleoidis-Veronicetum spicatae Br.-Bl. 1963 p. p. [Art. 37], Gypsophilo-Globularietum (Br.-Bl. 1963) Krahulec et al. 1986 [Art. 3b]

Note: Following ICPN Art. 37, the name Phleo phleoidis-Veronicetum spicatae Br.-Bl. 1963 is rejected as a *nomen dubium* because we consider the five relevés on which it is based to be too incomplete and too complex to be assigned to associations in the recent system (cf. DENGLER et al. 2003: 608). Because of their large size (mostly 50 m²), they probably comprise mosaics of our association with the Veronico spicatae-Avenetum Krahulec et al. 1986 nom. inval. (class: Festuco-Brometea).

Appendix 2. Type relevés that have not yet been published. Within each stratum, taxa are ordered according to their cover-abundance values. Character taxa of the associations are set in bold face.

Rel. A [= neotype of the *Cladonio-Sedetum*]

Source: This relevé is one of the five on which TÜXEN (1951) based his synoptic table of the association. It was kindly supplied by the Tüxen archive in Hannover (original handwritten number: 315) – Date: 16.07.1950 – Location: Sweden: Uppland: island of Runmarö – Site conditions: exposition: 15° W – Plot size: 2 m² – Species richness: total: 12, vascular plants: 7, bryophytes: 3, lichens: 2 [our experience leads us to consider this species list as rather incomplete; since, however, the assignment to this association is clear, it can nevertheless serve as the nomenclatural type].

Field layer: *Sedum album* 4; *Allium oleraceum* 2; *Allium schoenoprasum* var. *schoenoprasum* 2; *Sedum acre* 1; *Sedum telephium* 1; *Bromus hordeaceus* ssp. *hordeaceus* +; *Myosotis ramosissima* ssp. *ramosissima* +

Cryptogam layer: *Tortula ruralis* agg. 3; *Ditrichum flexicaule* 2; *Peltigera rufescens* 2; *Thuidium abietinum* 2; *Cladonia symphycarpa* 1

Rel. B [= holotype of the *Crepido-Allietum*]

Source: LÖBEL (2002: rel. A54) – Date: 01.06.2001 – Location: Sweden: Öland: Great Alvar; Coordinates (Swedish grid): 1 548 163/6 267 828 – Site conditions: cattle pasture, flat, microtopography: 2 cm, soil depth: 8 cm, pH (H₂O) = 7.7, pH (KCl) = 7.5 – Vegetation structure: plant cover total: 90 %, field layer: 85 %, cryptogam layer: 65 %, bare rock: 0 % – Plot size: 4 m² – Species richness: total: 56, vascular plants: 22, bryophytes: 27, lichens: 6; “algae”: 1.

Field layer: *Allium schoenoprasum* var. *alvarense* 3; *Prunella vulgaris* 3; *Artemisia rupestris* 2a; *Festuca ovina* 2a; *Sedum album* 2a; *Achillea millefolium* ssp. *millefolium* 1; *Acinos arvensis* 1; *Agrostis stolonifera* 1; *Artemisia campestris* ssp. *campestris* 1; *Cerastium pumilum* 1; *Crepis tectorum* ssp. *pumila* 1; *Festuca oelandica* 1; *Hieracium ×dichotomum* 1; *Poa compressa* 1; *Rhinanthus minor* 1; *Leontodon autumnalis* +; *Ranunculus bulbosus* ssp. *bulbosus* +; *Sedum rupestre* +; *Daucus carota* ssp. *carota* r; *Hieracium pilosella* r; *Plantago lanceolata* r; *Taraxacum officinale* agg. r

Cryptogam layer: *Hypnum cupressiforme* var. *lacunosum* 2b; *Ctenidium molluscum* 2a; *Ditrichum flexicaule* 2a; *Fissidens dubius* 2a; *Scorpidium turgescens* 2a; *Bacidia bagliettoana* 2m; *Barbula convoluta* 2m; *Bryum* sp. 2m; *Calliergonella cuspidata* 2m; *Campyllum chrysophyllum* 2m; *Cladonia foliacea* 2m; *Cladonia rangiformis* 2m; *Cladonia symphycarpa* 2m; *Didymodon fallax* 2m; *Didymodon ferrugineus* 2m; *Distichium capillaceum* 2m; *Distichium inclinatum* 2m; *Ecnalypa vulgaris* 2m; *Fissidens taxifolius* 2m; *Homalothecium lutescens* 2m; *Leptogium lichenoides* 2m; *Leptogium schraderi* 2m; *Mannia pilosa* 2m; *Nostoc* sp. 2m; *Pleuridium* cf. *acuminatum* 2m; *Poblia wahlenbergii* 2m; *Schistidium* sp. 2m; *Thuidium abietinum* 2m; *Tortella tortuosa* 2m; *Trichostomum crispulum* 2m; *Weissia brachycarpa* 2m; *Weissia squarrosa* 2m; *Athalamia hyalina* 1; *Campyllum calcareum* 1

Rel. C [= holotype of the *Helianthemo-Galietum*]

Source: LÖBEL (2002: rel. A78) – Date: 02.07.2001 – Location: Sweden: Öland: Great Alvar; Coordinates (Swedish grid): 1 541 218/6 264 806 – Site conditions: sheep and horse pasture, flat, microtopography: 0 cm, soil depth: 6 cm, pH (H₂O) = 7.9, pH (KCl) = 7.6 – Vegetation structure: plant cover total: 50 %, field layer: 40 %, cryptogam layer: 15 %, bare rock: 5 %

bare rock: 30 % – Plot size: 4 m² – Species richness: total: 56, vascular plants: 22, bryophytes: 19, lichens: 15.

Field layer: *Festuca ovina* 2a; *Helianthemum oelandicum* ssp. *oelandicum* 2a; *Hieracium pilosella* 2a; *Orchis mascula* ssp. *mascula* 2a; *Sisymbrium supinum* 2a; *Thymus serpyllum* ssp. *serpyllum* 2a; *Linum catharticum* 2m; *Anagallis arvensis* 1; *Carex flacca* ssp. *flacca* 1; *Euphrasia stricta* 1; *Galium oelandicum* 1; *Sedum album* 1; *Agrostis stolonifera* +; *Asperula tinctoria* +; *Carlina vulgaris* ssp. *vulgaris* +; *Crepis tectorum* ssp. *pumila* +; *Potentilla tabernaemontani* +; *Silene uniflora* ssp. *petraea* +; *Anthyllis vulneraria* ssp. *vulneraria* r; *Gypsophila fastigiata* r; *Orchis morio* ssp. *morio* r; *Taraxacum erythrospermum* agg. r
Cryptogam layer: *Cladonia arbuscula* 2b; *Tortella tortuosa* 2a; *Bacidia bagliettoana* 2m; *Bryum capillare* 2m; *Bryum elegans* 2m; *Cetraria aculeata* 2m; *Cetraria ericetorum* ssp. *ericetorum* 2m; *Cladonia foliacea* 2m; *Cladonia rangiformis* 2m; *Cladonia subrangiformis* 2m; *Cladonia symphylicarpa* 2m; *Collema* cf. *auriforme* 2m; *Collema tenax* 2m; *Ctenidium molluscum* 2m; *Distichium capillaceum* 2m; *Ditrichum flexicaule* 2m; Cf. *Ditrichum* sp. 2m; *Encalypta vulgaris* 2m; *Fissidens dubius* 2m; *Grimmia pulvinata* 2m; *Hypnum cupressiforme* var. *lacunosum* 2m; *Leptogium lichenoides* 2m; Lichen species, indet. (gray-green) 2m; *Pleuridium* cf. *acuminatum* 2m; *Scapania calcicola* 2m; *Schistidium robustum* 2m; *Scorpidium turgescens* 2m; *Thuidium abietinum* 2m; *Tortella rigens* 2m; *Tortula calcicolens* 2m; *Cetraria islandica* 1; *Cetraria nivalis* 1; *Thamnochloa vermicularis* var. *subuliformis* 1
Epilithic stratum: *Grimmia pulvinata* 2m; *Schistidium atrofusum* 2m

Rel. D [= holotype of the Gypsophilo-Globularietum]

Source: LÖBEL (2002: rel. A22) – Date: 01.06.2001 – Location: Sweden: Öland: Great Alvar; Coordinates (Swedish grid): 1 539 805/6 270 062 – Site conditions: cattle pasture, flat, microtopography: 5 cm, soil depth: 1–10 cm, pH (H₂O) = 7.3, pH (KCl) = 7.3 – Vegetation structure: plant cover total: 70 %, field layer: 60 %, cryptogam layer: 50 %, bare rock: 10 % – Plot size: 4 m² – Species richness: total: 58, vascular plants: 28, bryophytes: 22, lichens: 8.

Field layer: *Globularia vulgaris* 2b; *Thymus serpyllum* ssp. *serpyllum* 2b; *Festuca ovina* 2a; *Gypsophila fastigiata* 2a; *Oxytropis campestris* ssp. *campestris* 2a; *Acinos arvensis* 1; *Asperula tinctoria* 1; *Campanula rotundifolia* 1; *Carex ericetorum* 1; *Cerastium pumilum* 1; *Erophila verna* 1; *Hieracium pilosella* 1; *Sedum acre* 1; *Sedum album* 1; *Anthyllis vulneraria* ssp. *vulneraria* +; *Arabis hirsuta* var. *glaberrima* +; *Artemisia campestris* ssp. *campestris* +; *Avenula pratensis* ssp. *pratensis* +; *Filipendula vulgaris* +; *Helianthemum oelandicum* ssp. *oelandicum* +; *Hornungia petraea* +; *Hypochoeris maculata* +; *Medicago lupulina* +; *Polygala comosa* +; *Potentilla tabernaemontani* +; *Saxifraga tridactylites* +; *Scabiosa columbaria* ssp. *columbaria* +; *Taraxacum erythrospermum* agg. +

Cryptogam layer: *Cladonia pyxidata* agg. 2a; *Cladonia rangiformis* 2a; *Amblystegium varium* 2m; *Athalamia hyalina* 2m; *Barbula convoluta* 2m; *Bryum* sp. 2m; *Campylopus chrysophyllum* 2m; *Cetraria aculeata* 2m; *Cetraria islandica* 2m; *Cladonia arbuscula* 2m; *Cladonia foliacea* 2m; *Cladonia subrangiformis* 2m; *Dicranum scoparium* 2m; *Ditrichum flexicaule* 2m; *Encalypta vulgaris* 2m; *Fissidens dubius* 2m; *Grimmia pulvinata* 2m; *Homalothecium lutescens* 2m; *Hypnum cupressiforme* var. *lacunosum* 2m; *Schistidium* sp. 2m; *Tortella inclinata* 2m; *Tortella tortuosa* 2m; *Tortula calcicolens* 2m; *Trichostomum crispulum* 2m; *Weissia brachycarpa* 2m; *Lophozia excisa* 1; *Myurella julacea* 1; *Rhytidium rugosum* 1; *Tortula ruraliformis* 1; *Peltigera rufescens* r

Appendix 3. Nordic relevés from other sources included in this study. The countries are indicated by their international abbreviations.

Source	Table no.	Syntaxon name (in source)	Geographic origin	Criterion for inclusion of relevés	No. of relevés included	Relevé area(s)
DENGLER & RIXEN (unpubl. report 1995)	B	<i>Alysso alyssoidis-Sedetum albi</i>	S: northern Öland: Hornsudden	relevés with given plot size	3	4 m ²
DU RIETZ (1925)	p. 33	<i>Sedum-Cetraria islandica</i> -Ass.	S: Gotland: Hejdby Häller	all	2*	4 m ²
HALLBERG (1971)	13	Sedo-Tortelletum	S: Bohuslän	plot size ≥ 2 m ²	13	2 m ²
HALLBERG (1971)	14	Ditricho-Sedetum	S: Bohuslän	plot size ≥ 2 m ²	15	2–8 m ²
HALLBERG (1971)	15	<i>Arenaria serpyllifolia-Sedum acre</i> -Gesellschaft	S: Bohuslän	plot size ≥ 2 m ²	14	2–6 m ²
HALLBERG (1971)	15	<i>Ditrichum flexicaule</i> -Gesellschaft	S: Bohuslän	plot size ≥ 2 m ²	1	4 m ²
MARKER (1969)	III	Sedetum acris	N: Telemark: Langöya	all	11	10 m ²
MARKER (1969)	IV	<i>Poo alpinae-Anthyllidetum vulnerariae typicum</i>	N: Telemark: Langöya	plot size ≤ 10 m ²	3	10 m ²
original relevés of TÜXEN (1951)	7	Sedo albi-Cladonietum symphyrcarpae	S: Uppland: Runmarö	relevé no. 315 in the Tüxen archive	1	2 m ²
WESTHOFF et al. (1983)	5	<i>Alysso-Sedion</i>	S: Gotland: Stora Karlsö	relevé no. 5	1	5 m ²
WESTHOFF et al. (1983)	5	<i>Helianthemoglobularion</i>	S: Gotland: Stora Karlsö	relevé no. 9	1	10 m ²

* Since we have found these relevés after the completion of the paper, they have only been included in the phytosociological table and not in the numerical analyses.

Appendix 4. Central European relevés included in this study. The countries are indicated by their international abbreviations.

Source	Table no.	Syntaxon name (in source)	Geographic origin	Criterion for inclusion of relevés	No. of relevés included	Relevé area(s)
BECKER (1998)	2	Poo badensis-Allietum montani	D: Saxony-Anhalt: Unstrut valley	$2 \text{ m}^2 \leq \text{plot size} \leq 10 \text{ m}^2$	5	2.1–7 m ²
BORNKAMM (1961)	7	<i>Sedum</i> -Gesellschaften	D: Lower Saxony: Göttingen	plot size $\geq 2 \text{ m}^2$ except for those with <i>Sedum spurium</i>	10	2–6 m ²
BRAUN-BLANQUET (1961)	6	Sedetum brigantiacum	F: Durance valley; I: Aosta valley	all	26	4–10 m ²
DENGLER (unpubl. report 2001)	p. 171	Alyso alyssoidis-Sedion albi	CH: Grisons: Davos	–	1	10 m ²
DENGLER & BERG (unpubl.)		Saxifrago tridactylitae-Poetum compressae	D: Mecklenburg-Vorpommern	–	3	10 m ²
GAUCKLER (1957)	3	Fulgensio fulgentis-Lecanoretum lentigerae	D: Bavaria: Unterfranken	plot size $\geq 2 \text{ m}^2$	3	2–10 m ²
JANDT (1999)	15	Cerastietum pumili	D: Southern part of Harz mountains	plot size $\leq 10 \text{ m}^2$	3	4–8 m ²
JANDT (1999)	16	<i>Cladonia foliacea</i> -Gesellschaft	D: Southern part of Harz mountains	plot size $\leq 10 \text{ m}^2$	1	9 m ²
KORNECK (1974)	44	Saxifrago-Poetum compressae	D: Rhineland-Palatinate: Ochtendung	–	1	3 m ²
KORNECK (1974)	45	<i>Androsace elongatae</i> -Gesellschaft	D: Hesse: Wonsheim	plot size $\geq 2 \text{ m}^2$	1	5 m ²
KORNECK (1975)	22	Tortello-Poetum concinnae	F: Durance valley; I: Susa	original relevés with plot sizes $\geq 2 \text{ m}^2$	8	2–8 m ²
KORNECK (1975)	23	Trisetetum cavanillesii	I: Aosta valley	plot size $\geq 2 \text{ m}^2$	4	2–3 m ²
KORNECK (1975)	24	Clypeoletum jonthlasi	CH: Valais: Visper valley	plot size $\geq 2 \text{ m}^2$	2	2 m ²
KORNECK (1975)	26	Cerastietum pumili	F: Burgundy	plot size $\geq 2 \text{ m}^2$	2	2 m ²
KORNECK (1975)	27	Cerastietum pumili	F: Alsace	plot size $\geq 2 \text{ m}^2$	2	2 m ²
KORNECK (1975)	30	Cerastietum pumili	D: Northern Bavaria	plot size $\geq 2 \text{ m}^2$	4	2–3 m ²
KORNECK (1975)	31	Cerastietum pumili	D: Eifel: Iversheim	relevé area $\geq 2 \text{ m}^2$	1	2 m ²

Appendix 4 (cont.)

Source	Table no.	Syntaxon name (in source)	Geographic origin	Criterion for inclusion of relevés	No. of relevés included	Relevé area(s)
KORNECK (1975)	33	<i>Alyso alyssoidis-Sedetum albi</i>	D: Bavaria: Fränkische Alb	plot size $\geq 2 \text{ m}^2$	1	2 m ²
KORNECK (1975)	34	<i>Poo badensis-Allietum montani</i>	D: Bavaria: Main valley	original relevés with plot sizes $\geq 2 \text{ m}^2$	12	2–10 m ²
KORNECK (1975)	36	<i>Sempervivetum soboliferi</i>	D: Bavaria: Fränkische Alb	plot size $\geq 2 \text{ m}^2$	2	2 m ²
KORNECK (1975)	37	<i>Minuartia glomerata</i> -Gesellschaft	SK: near Kamenica nad Hronom	plot size $\geq 2 \text{ m}^2$	1	2 m ²
MARQUARDT et al. (2004)	11	<i>Saxifraga tridactylites</i> - <i>Poetum compressae</i>	D: Lower Saxony: Lüneburg	relevés with <i>Saxifraga tridactylites</i>	5	4 m ²
PHILIPPI (1984)	p. 574	<i>Cerastietum pumili</i>	D: Baden-Württemberg: Renz valley	–	1	2 m ²
REBELE (1986)	20	<i>Sedum acre</i> -Rasen	D: Berlin	relevé no. 1	1	4 m ²
ULLMANN (1977)	31	<i>Cerastietum pumili</i>	D: Bavaria: Main valley	–	1	6 m ²
ULLMANN (1977)	31	<i>Allium oleraceum-Sedum</i> -Gesellschaft	D: Bavaria: Main valley	relevé area $\geq 2 \text{ m}^2$	6	2–10 m ²
WITTIG & LIENENBECKER (2003)	8a	<i>Saxifraga tridactylites</i> - <i>Poetum compressae</i>	D: Eastern Westphalia	except for relevés with dominant <i>Bromus tectorum</i>	9	2–4 m ²
WITTIG & LIENENBECKER (2003)	8b	<i>Saxifraga tridactylites</i> -Gesellschaft	D: Eastern Westphalia	every 2 nd relevé $\geq 2 \text{ m}^2$ except for those with dominant <i>Bromus sterilis</i>	11	2–4 m ²