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## Dry grassland communities of shallow, skeletal soils (*Sedo-Scleranthenea*) in northern Europe

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### Abstract

We studied the dry grasslands of shallow, skeletal soils (*Sedo-Scleranthenea*, *Koelerio-Corynephoretea*) in northern Europe, based on a combination of new relevés from southern Öland (Sweden,  $n = 182$ ) and Saaremaa (Estonia,  $n = 73$ ) as well as a comprehensive evaluation of literature data, of which 65 suitable relevés were directly included in our analyses. Apart from a few vague indications of acidophytic *Sedo-Scleranthenea* communities (order *Sedo-Scleranthetalia*), all data refer to basiphytic communities (*Alyso-Sedetalia*); our analyses are thus focussed on the latter. The Nordic *Alyso-Sedetalia* communities proved to be quite different from their temperate counterparts and thus are included in a separate alliance, *Tortello tortuosae-Sedion albi*, which forms the northern counterpart to the central European *Alyso-Sedion*. Within the northern alliance, we distinguish two suballiances. The more widespread central suballiance *Tortello tortuosae-Sedenion albi* inhabits different types of base-rich substrata in both natural and anthropogenic sites, and is comprised of the *Cladonio symphicarpiæ-Sedetum albi* and the *Ditricho flexicaulis-Sedetum acris*. The second suballiance *Tortello rigentis-Helianthemion oelandici* is restricted to the alvar sites (= treeless limestone plateaus) in Öland, Gotland, Västergötland and Estonia. It is characterised by several endemic taxa and a large number of cryptogams typical of alvar. It is comprised of four associations, *Crepido pumilæ-Allietum alvarensis*, *Fulgensio bracteatae-Poetum alpinae*, *Helianthemo oelandici-Galietum oelandici* and *Gypsophilo fastigiatae-Globularietum vulgaris*. All six Nordic associations are described in detail with respect to their floristic composition, ecology, distribution and lower-ranked units, and each is represented by a vegetation table. The floristic differences within the Nordic communities are worked out in a synoptic table. Whereas several vegetation scientists have pointed out that vegetation types occurring at the limits of their distribution ranges in northern Europe are generally difficult to classify, our application of the Braun-Blanquet approach, which is based on *a priori* separated structural types and the general application of the central syntaxon concept, has enabled us to characterise and adequately define all Nordic communities. The *Tortello-Sedion* associations are two to three times as species-rich as those of the *Alyso-Sedion* and are among the most diverse small-scale plant communities ever described. We discuss the reasons for this exceptionally high plant diversity and the peculiar species mixture in the *Tortello-Sedion* and compare the relationship between *Alyso-Sedion* and *Tortello-Sedion* to the situation of other Nordic syntaxa of predominantly temperate vegetation types. Our results further underline the uniqueness of Baltic alvars and their paramount importance for conservation at the European level.

### Zusammenfassung: Felsgrusgesellschaften (*Sedo-Scleranthenea*) im nördlichen Europa

Wir haben die Felsgrusgesellschaften (*Sedo-Scleranthenea*, *Koelerio-Corynephoretea*) Nordeuropas auf der Basis eigener Aufnahmen aus Süd-Öland (Schweden,  $n = 182$ ) und Saaremaa (Estland,  $n = 73$ ) sowie einer umfassenden Auswertung der Literatur (davon fanden 65 geeignete Aufnahmen unmittelbar in den Analysen Verwendung) untersucht. Abgesehen von spärlichen und vagen Hinweisen auf bodensaure *Sedo-Scleranthenea*-Gesellschaften (*Sedo-Scleranthetalia*) beziehen sich alle verfügbaren Daten auf basiphytische Typen (*Alyso-Sedetalia*), weswegen wir uns im Kern mit diesen beschäftigen. Die nordischen *Alyso-Sedetalia*-Gesellschaften unterscheiden sich erheblich von ihren in der temperaten Zone verbreiteten Pendanten. Daher stellen wir sie als eigenen Verband *Tortello tortuosae-Sedion albi* dem mitteleuropäischen *Alyso-Sedion* gegenüber. Innerhalb des nordischen Verbandes lassen sich zwei Unterverbände trennen. Der relativ weit verbreitete zentrale Unterverband *Tortello tortuosae-Sedenion albi* besiedelt unterschiedliche basenreiche Substrate sowohl natürlichen als auch anthropogenen Ursprungs. Der zweite Unterverband *Tortello rigentis-Helianthemion oelandici* ist auf die Alvare (= baumfreie Kalksteinplateaus) in Öland, Gotland, Västergötland und Estland beschränkt. Er ist durch eine Reihe endemischer Sippen sowie viele alvartypische Kryptogamen gekennzeichnet und umfasst vier Assoziationen: *Crepido pumilæ-Allietum alvarensis*, *Fulgensio bracteatae-Poetum alpinae*, *Helianthemo oelandici-Galietum oelandici* und *Gypsophilo fastigiatae-Globularietum vulgaris*. Die sechs nordischen

Assoziationen werden detailliert bezüglich floristischer Zusammensetzung, Ökologie, Verbreitung und Untergliederung beschrieben und mit je einer Vegetationstabelle präsentiert. Die floristischen Unterschiede der nordischen Gesellschaften untereinander illustrieren wir in einer Stetigkeitstabelle. Zwar haben verschiedene Vegetationskundler in der Vergangenheit darauf hingewiesen, dass es generell schwierig sei, Vegetationstypen zu klassifizieren, die in Nordeuropa am Rande ihres Synareals vorkommen, doch ermöglichte unsere Konkretisierung des Braun-Blanquet-Ansatzes, die auf einer strukturtypenbezogenen Klassifikation und der Anwendung des Zentralsyntaxonkonzeptes auf allen hierarchischen Ebenen beruht, eine sachgerechte Charakterisierung und Klassifizierung aller in Nordeuropa vorkommenden Typen. Die Artendichte in den *Tortello-Sedion*-Assoziationen ist zwei- bis dreimal so hoch wie im *Alyso-Sedion*, womit die basiphilen Felsgrusgesellschaften Nordeuropas zu den auf kleinen Flächen artenreichsten Vegetationstypen überhaupt gehören. Wir diskutieren Gründe der herausragenden Phytodiversität und der eigentümlichen Artenzusammensetzung des *Tortello-Sedion* und vergleichen die Unterschiede zwischen *Tortello-Sedion* und *Alyso-Sedion* mit der Situation in anderen nordischen Syntaxa. Unsere Ergebnisse unterstreichen die Einzigartigkeit der baltischen Alvargesellschaften und ihre herausragende Bedeutung für den Naturschutz auf europäischer Ebene.

**Keywords:** Alvar vegetation, *Alyso-Sedetalia*, Öland (Sweden), Saaremaa (Estonia), syntaxonomy, species richness, *Tortello tortuosae-Sedion albi*.

## 1. Introduction

Within the *Koelerio-Corynephoretea*, the subclass *Sedo-Scleranthenea* inhabits sites with very thin residual soils over massive bedrock or gravel (DENGLER et al. 2003). These communities are especially rich in succulents, therophytic vascular plants, bryophytes and lichens. In central Europe, these so-called ‘weathered rock and outcrop communities’ were introduced to syntaxonomy by BRAUN-BLANQUET (1955) and MÜLLER (1961). Since then, a number of extensive studies have been devoted to them (BRAUN-BLANQUET 1961, MORAVEC 1967, KORNECK 1975), and they find their place in all of the recent phytosociological overviews (e.g. MUCINA & KOLBEK 1993, POTT 1995, SCHAMINÉE et al. 1996b, SCHUBERT et al. 2001) though they are treated at different hierarchical levels. In northern Europe, by contrast, similar communities have been studied for a much longer time, with the first detailed descriptions (mostly already with relevés) going back to DU RIETZ (1925: Gotland), STERNER (1925: Öland), VILBERG (1927: Estonia) and ALMQUIST (1929: Uppland). This early attention may have been caused by the fact that in northern Europe *Sedo-Scleranthenea* communities cover rather huge areas in the so-called alvars (= treeless limestone plateaus), whereas their central European counterparts typically occur on patches of few square metres or less, in between other dry grassland communities.

ALBERTSON (1946, 1950) was the first to give a comprehensive overview and classification of the dry grassland types inhabiting two of the major alvar regions. In his local studies, he distinguished three main types, of which the ‘*Sedetum*’ and the ‘*Festucetum*’ largely correspond to the *Sedo-Scleranthenea* whereas the ‘*Avenetum*’ belongs to the *Festuco-Brometea* Br.-Bl. & Tx. ex Klika & Hadač 1944. Even today, Swedish and Estonian geobotanists often refer to ALBERTSON’s coarse and nomenclaturally invalid units in their studies (e.g. ROSÉN 1982, PÄRTEL et al. 1999a). There have been some attempts by geobotanists from abroad to ‘append’ the Nordic dry grassland communities of shallow skeletal soils to the syntaxonomic system developed in central Europe (BRAUN-BLANQUET 1963, WESTHOFF et al. 1983, ROYER 1991, DIERBEN 1996) but as these authors relied on literature data or at best a few relevés of their own they essentially failed to capture the distinctness of the Nordic communities. A well-founded formal classification of the Nordic *Sedo-Scleranthenea* has thus been lacking and, as a consequence, overviews of vegetation types in the Nordic countries for the most part still tend to characterise such vegetation types using informal units such as ‘*Sedum album-Tortella* spp.-typ’. In most cases, these types are only vaguely described by mentioning some typical species and are not backed up by vegetation tables (e.g. NORDISKA MINISTERRÅDET 1984, FREMSTAD 1997, PÅHLSSON 1999, ROSÉN & BORGEGÅRD 1999).

Recently, two of us filled this gap by presenting a supraregional syntaxonomic classification of the basiphilous *Sedo-Scleranthenea* communities (order: *Alyso alyssoidis-Sedetalia*)

of northern Europe based on new relevés from Öland and a synthesis of literature data from other regions (DENGLER & LÖBEL 2006). The Nordic *Alyso-Sedetalia* communities proved to be floristically quite different from their southern counterparts and thus were placed in an alliance of their own, *Tortello tortuosae-Sedion albi*, with two suballiances and six associations. They also proved to have a peculiar species mixture, bringing together arctic-alpine and Mediterranean or eastern steppe species as well as those tolerant to extreme drought stress with others that are adapted to temporarily moist soils. In addition, the associations of the *Tortello-Sedion* are of great interest to biodiversity research as they show exceptionally high small-scale species richness.

Since the publication of DENGLER & LÖBEL (2006), new literature data has become available and BOCH (2005) conducted a phytosociological study of the dry grasslands on the Estonian island of Saaremaa, similar to that of LÖBEL (2002) on Öland. Besides making available the comprehensive data base of these two diploma theses to an international audience, we wish to address the following questions with the present paper:

- Is the classification of DENGLER & LÖBEL (2006) also applicable to Estonia?
- How are the *Sedo-Scleranthenea* communities distributed in northern Europe and how can they be subdivided?
- What are the differences between the Nordic and central European *Sedo-Scleranthenea* communities? What are the reasons and syntaxonomic implications of these differences?
- Are the gradients in community distinctness, species pool size and species densities between central and northern Europe in the *Sedo-Scleranthenea* similar or different from other vegetation types?

## 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. *Sedo-Scleranthenea* communities are largely restricted to the southern part of northern Europe, namely the nemoral and boreonemoral zones.

The Baltic Shield, comprising Finland, most of Sweden and Norway east of the Scandes, has very old, mainly siliceous bedrock (e.g. SJÖRS et al. 2004). Southeast of the Shield, on the Swedish islands of Öland and Gotland as well as in some smaller parts of the Swedish provinces Öster- and Västergötland, in Estonia and in the adjacent part of Russia, however, calcareous sediments of the Ordovician and Silurian age cover this Precambrian stratum (e.g. EMBLETON 1984). Sites where this limestone bedrock is close to the surface or even exposed and that are therefore only sparsely covered by vegetation are referred to as 'alvars' in the ecological literature (ALBERTSON 1946, ZOBEL & KONT 1992). Within the Shield, only a small percentage of the area is affected by calcareous minerals, especially in southeastern Norway (SJÖRS et al. 2004). In addition, highly calcareous tills on top of non-calcareous bedrock provide base-rich substrata in northern Uppland (Sweden) and Åland (Finland), as do in some places marine shell-deposits, which are now on land (SJÖRS et al. 2004). Besides the alvar areas and the Scandes, superficial bedrock for the most part is limited to areas near the seacoast (EMBLETON 1984, TYLER 1996).

The climate of the southern part 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. In 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 (file worldclim\_10m; cf. NEW et al. 2002). However, July temperatures are quite uniform with means of 15–17° C throughout most of the region (SJÖRS et al. 2004).

## 2.2. Southern Öland

Shallow calcareous soils in northern Europe reach their greatest extension in the southern part of the Swedish island of Öland. The so-called Great Alvar is a flat plateau of Ordovician limestone in the centre of the island that covers more than 200 km<sup>2</sup> (KÖNIGSSON 1968). Compared to other calcareous bedrocks, the Ordovician limestone on Öland is especially hard with horizontal layers (e.g. KRAHULEC et al. 1986, STERNER & LUNDQVIST 1986). Whereas in most parts of the island, the bedrock is covered by quaternary deposits (e.g. STERNER & LUNDQVIST 1986), in the Great Alvar and other smaller alvar areas, these are relatively thin and partly absent. Here, lime-poor soils over moraines and post-glacial shore ridges alternate with weathered soils of varying thickness (1–15 cm) originating from the limestone bedrock, and on a small percentage of the area the limestone rock is totally bare and locally shows karst phenomena (KÖNIGSSON 1968, KRAHULEC et al. 1986).

While the temperature regime on Öland is rather oceanic with a mean annual temperature of 7.0 °C (February –0.4 °C, July 16.6 °C, DENGLER & LÖBEL 2006), the annual precipitation varies from less than 450 mm in the coastal to 500 mm in the central parts of the island with especially low values in summer (e.g. KRAHULEC et al. 1986, STERNER & LUNDQVIST 1986). In addition, precipitation varies considerably from year to year. Strong winds often intensify the drying-out of the thin soils in summer, whereas in autumn and spring the poor drainage of the compact limestone plateau leads to extensive inundations. During late autumn and early spring, such water-saturated soils can be strongly affected by frost-induced soil movement, leading partly to polygon soils and partly to a distinctive microrelief (ALBERTSON 1950, KÖNIGSSON 1968, ROSÉN 1982, KRAHULEC et al. 1986).

The island was first colonised by humans 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, DIERBEN 1996). Grazing, small-scale agriculture and firewood cutting over many centuries have effectively kept back shrub- and woodland (KRAHULEC et al. 1986, ROSÉN & VAN DER MAAREL 2000).

Our study area (c. 280 km<sup>2</sup>; 56° 30' N, 16° 30' E) comprises the northern part of southern Öland, including about half of the Great Alvar. The villages Färjestaden and N Möckleby form its northern corners, and Mörbylånga and Alby its southern corners (see DENGLER & LÖBEL 2006).

## 2.3. Saaremaa

In Estonia, we studied *Sedo-Scleranthenea* communities on the Baltic island of Saaremaa (2,673 km<sup>2</sup>; 57° 50'–58° 40' N, 21° 45'–23° 20' E). The bedrock of this island is formed by Silurian limestone (RAUKAS & TEEDUMÄE 1997), that is located in part close to the surface but more often is covered by Weichselian moraines or Holocene marine sediments (POSKA & SAARSE 2002). Dry alvar areas are mainly distributed in the western part of the island, including the peninsula of Sörve and the national park of Vilsandi, but some smaller patches occur all over the island. The soils are predominantly silt or clay and have a high humus content. Outside the alvars, *Sedo-Scleranthenea* communities also occur on (fossil) shore ridges and anthropogenic substrata such as stone embankments, concrete slabs and gravel.

The mean annual temperature is about 6.0 °C, with the continental influence resulting in considerably lower winter temperatures than on Öland (in February ranging from –3.5 °C in the west to –5.0 °C in the east; ANONYMOUS 1970). The annual precipitation on Saaremaa varies between 540 mm and 675 mm (RAUDSEPP & JAAGUS 2002).

Indications of the first permanent settlements on the island were found in the alvar regions and originate from the Mesolithicum (5,000 to 4,000 B.C.; LÖUGAS 1988). The alvar grasslands were used for livestock grazing for many centuries but at present most of these areas have been abandoned and are thus subject to succession and overgrowth (cf. PÄRTEL et al. 1999b, HELM et al. 2006).

### 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 & CRUNDWELL (1991) for mosses, GROLE & LONG (2000) for liverworts, and SANTESSON et al. (2004) 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): *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. cryptochlorophaea*, *C. grayi*, *C. merochlorophaea*, *C. monomorpha*, *C. novochlorophaea* and *C. pyxidata*, to a small extent probably also *C. pocillum*). The hybrid *Potentilla cinerea* x *tabernaemontani* is given as *Potentilla* x *subarenaria* Borbás ex Zimmeter. Finally, we recognise the following additional taxa because of their possible phytosociological importance: *Allium schoenoprasum* var. *alvarense* Hyl. and var. *schoenoprasum* (STERNER & LUNDQVIST 1986, JONSELL & KARLSSON 2004), *Arabis hirsuta* var. *glaberrima* Wahl. and var. *hirsuta* (STERNER & LUNDQVIST 1986), *Pimpinella saxifraga* subsp. *nigra* (Mill.) Gaudin and subsp. *saxifraga* (MOSSBERG & STENBERG 2003), *Silene uniflora* subsp. *petraea* (Fr. ex Hartm.) Jonsell & H. C. Prent. (JONSELL 2001), *Thalictrum simplex* subsp. *arenarium* (Butcher) Clapham in Clapham et al. (JONSELL 2001), *Hypnum cupressiforme* var. *cupressiforme* and var. *lacunosum* Brid. (KOPERSKI et al. 2000), *Pottia conica* (Schwägr.) Nyholm (NYHOLM 1989) and *Tortula calcicolens* Kramer (NYHOLM 1989).

#### 3.2. New relevés from Öland and Saaremaa

During spring and summer 2001, we sampled 469 phytosociological relevés of dry grassland communities within the study area on Öland, and in summer 2004, we did the same for the whole island of Saaremaa ( $n = 231$ ). The plots were distributed representatively over the dry grasslands within the two study areas, with the aim to include the full range of site conditions and floristic composition. In the final classification, we assigned 182 of the Ölandic and 73 of the Estonian relevés to the *Sedo-Scleranthenea*. Plot coordinates were determined with a Global Positioning System (GPS). GPS coordinates are listed alongside other plot data in LÖBEL (2002) and BOCH (2005), available at the University Library of Lüneburg.

Relevés were 4 m<sup>2</sup> in size throughout. All vascular plants, bryophytes, lichens and macroscopic 'algae' were recorded, including those of 'substrate strata', i.e. epiphytic, lignicolous and saxicolous taxa (cf. DENGLER 2003: 136). In the case of Öland, however, saxicolous crustose lichens were excluded because of determination problems. On Öland, abundance was estimated according to the Braun-Blanquet cover-abundance scale using the modified version of WILMANN'S (1998), whereas on Saaremaa we switched to the pure cover-scale of DENGLER (2003) because the first scale had posed problems in some numerical evaluations of the data (Table 2). For each relevé, several environmental and structural parameters were recorded (see DENGLER & LÖBEL 2006). They are used for the description of the associations in section 5; a detailed comparison between these is included in DENGLER & LÖBEL (2006).

#### 3.3. Relevé data 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 relevés (cf. JANDT & BRUELHEIDE 2002: 120, DENGLER 2003: 69). However, since this fact has rarely been considered in phytosociology, only a few relevés of equal size were available. We therefore decided to include relevés with plot sizes ranging from 2 to 10 m<sup>2</sup>, i.e. those close to our own plot size of 4 m<sup>2</sup>.

We attempted to include all suitable records from northern Europe ( $n = 65$ ; see Table 1) directly in our classification and in the tables, except for those from southern Öland where we had sufficient material of our own.

For the evaluation of the overall distribution of the syntaxa, we also used plot data that did not comply with the above two criteria (too small, too big, without cryptogam treatment) alongside all other available information (species distribution data, species lists). However, because these additional sources lack important information we are only able to present probable assignments to certain associations.

Table 1: Nordic relevés from other sources included in this study. The countries are indicated by their international abbreviations.

Tab. 1: Nordische Aufnahmen aus der Literatur, die in den Analysen einbezogen wurden. Die Länder sind mit ihrem internationalen Autokennzeichen angegeben.

Source	Table no.	Syntaxon name (in source)	Geographic origin	Included relevés	No. of relevés included	No. in this paper	Plot size(s)
DENGLER & RIXEN (1995)	B	<i>Alysso alyssoidis-Sedetum albi</i>	S: northern Öland: Hornsuden	relevés with plot size given	3	J01–J03	4 m <sup>2</sup>
DU RIETZ (1925)	p. 33	<i>Sedum-Cetraria islandica</i> -Ass.	S: Gotland: Hedby Hällar	all	2	J34–J35	4 m <sup>2</sup>
HALLBERG (1971)	13	<i>Sedo-Tortelletum</i>	S: Bohuslän	plot size ≤ 2 m <sup>2</sup>	13	–	2 m <sup>2</sup>
HALLBERG (1971)	14	<i>Ditricho-Sedetum</i>	S: Bohuslän	plot size ≤ 2 m <sup>2</sup>	15	–	2–8 m <sup>2</sup>
HALLBERG (1971)	15	<i>Arenaria serpyllifolia-Sedum acre</i> -Ges.	S: Bohuslän	plot size ≤ 2 m <sup>2</sup>	14	–	2–6 m <sup>2</sup>
HALLBERG (1971)	15	<i>Ditrichum flexicaule</i> -Ges.	S: Bohuslän	plot size ≤ 2 m <sup>2</sup>	1	–	4 m <sup>2</sup>
MARKER (1969)	III	<i>Sedetum acris</i>	N: Telemark: Langöya	all	11	J04–J14	10 m <sup>2</sup>
MARKER (1969)	IV	<i>Poo alpinae-Anthyllidetum vulnerariae typicum</i>	N: Telemark: Langöya	plot size ≤ 10 m <sup>2</sup>	3	J30–J32	10 m <sup>2</sup>
original relevés of TÜXEN (1951)	7	<i>Sedum album-Cladonia symphy carpia</i> -Ass.	S: Uppland: Runmarö	relevé no. 315 in the Tüxen archive	1	J29	2 m <sup>2</sup>
WESTHOFF et al. (1983)	5	<i>Alysso-Sedion</i>	S: Gotland: Stora Karlsö	relevé no. 5	1	J33	5 m <sup>2</sup>
WESTHOFF et al. (1983)	5	<i>Helianthemoglobularion</i>	S: Gotland: Stora Karlsö	relevé no. 9	1	J23	10 m <sup>2</sup>

### 3.4. Phytosociological methods

#### 3.4.1. Classification principles

In the phytosociological classification, we followed the consistent application of the Braun-Blanquet approach proposed by DENGLER (2003, see also DENGLER & BERG 2002). This combines the ideas of BERGMEIER et al. (1990) and the central syntaxon concept of DIERSCHKE (e.g. 1994: 324). We briefly outline only the most important aspects here:

- All phytocoenoses, including so-called ‘atypical’ or ‘fragmentary’ types, are taken into account for classification.
- The classification is carried out within three *a priori* separated structural types of vegetation: woodlands, herbaceous vegetation (including dwarf shrubs) and one-layered cryptogam vegetation.
- 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.
- As an exception, one taxon can be considered as 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’ are species that 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.
- The presence degree 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.

In our study, we only analysed phytocoenoses of the herbaceous vegetation. A stand was included when the total cover of the herb layer reached 5 % or the number of vascular plant individuals or ramets together was at least 50 (corresponding to the Braun-Blanquet category 2m) on 4 m<sup>2</sup>; 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 degree 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 (DIERBEN 1996) and Mecklenburg-Vorpommern (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.

### 3.4.2. Tablework and numerical analyses

Data entry, phytosociological tablework and the calculation of total and group-specific species numbers were carried out with SORT 4.0 (ACKERMANN & DURKA 1998). Before applying numerical analyses of the floristic relationships, we 'standardised' the data to keep distorting effects of different data quality as low as possible. For example, non-terricolous taxa (recorded only in a subset of the studies) and 'sp.'-data were excluded (for details, see DENGLER & LÖBEL 2006). We both applied cluster analyses, calculated by SORT 4.0 and using different (dis-)similarity indices and agglomeration procedures, and the TWINSPLAN algorithm (HILL 1979), implemented in the software package JUICE 6.3.45 (cf. TICHY 2002). These techniques were applied both for the delimitation of the associations within the whole data set and thereafter for the subdivision of these associations. Of the many potential classifications obtained, we selected those that were consistent across different numerical methods and that best agreed with the classification principles of section 3.4.1. Afterwards, some manual refinement was done with the aim to maximise the fidelity of the determined diagnostic taxa.

### 3.4.3. Phytosociological tables

In the phytosociological tables, we sometimes included uncertain species data ('cf.-data'). These are entered in the same line as the records determined with certainty and are printed in italics. The following abbreviations are used in the tables:

C	=	character species	V	=	vascular plant	Assoc.	=	association
D	=	differential species	B	=	bryophyte	Suball.	=	suballiance
		from association	L	=	lichen	All.	=	alliance
		upwards	A	=	'alga'	Ord.	=	order
d	=	differential species				Subcl.	=	subclass
		below association rank				Cl.	=	class
AD	=	differential species of the association						

In the association tables (Tables 4–8), the cover-abundance values are given either according to the classical scale of BRAUN-BLANQUET (1951) or its modification by WILMANN (1998) and DENGLER

Table 2: Explanation of the Braun-Blanquet categories in our own relevés from southern Öland and Saaremaa defined by abundance and dominance (as % coverage).

Tab. 2: Bedeutung der Braun-Blanquet-Kategorien in unseren eigenen Aufnahmen aus Süd-Öland und Saaremaa, definiert anhand von Individuenzahl und prozentualem Deckungsgrad.

Braun-Blanquet category	Meaning	
	Southern Öland (after WILMANN 1998)	Saaremaa (after DENGLER 2003)
r	> 0–5 %; 1 'individual'	> 0–1 %
+	> 0–5 %; 2–5 'individuals'	> 1–2.5 %
1	> 0–5 %; 6–50 'individuals'	> 2.5–5 %
2m	> 0–5 %; > 50 'individuals'	–
2a	> 5–15 %	> 5–10 %
2b	> 15–25 %	> 10–25 %

(2003; see Table 2). The records of MARKER (1969), who used the Domin scale, are therefore transformed to the most probable Braun-Blanquet category. The symbol 'v' stands for species that occur but whose cover-abundance value has not been estimated.

Relevés from the literature have a number starting with 'J'; their sources are listed in Table 1. 'SB' designates our relevés from Saaremaa:

SBK	=	Kaugatuma pank and Lõu pank	SBX	=	surroundings of Käräla; as far as Pidula laht to the north and Katri pank to the south
SBL	=	surrounding of Kihelkonna			
SBN	=	Nasva and alvar west of Kuressaare			
SBP	=	Papissaare ps	SBY	=	Ninase ps (Tagaranna pank) and Panga pank, as far as Poka to the east
SBV	=	island of Vilsandi	SBZ	=	surroundings of Valjala, as far as Kübassaare ps to the east

All other starting letters stand for Ölandic relevés:

A or T	=	Great Alvar	E	=	small alvar areas on the east coast
C	=	Western Landridge			

The geographic origin of the relevés is indicated in the header data as follows:

G	=	Gotland (main island, Sweden)	sÖ	=	southern Öland (Sweden)
nÖ	=	northern Öland (Sweden)	T	=	Telemark (Norway)
S	=	Saaremaa (Estonia)	U	=	Uppland (Sweden)
SK	=	Stora Karlsö (province Gotland, Sweden)			

In the synoptic table (Table 3), we present presence degree (reference) values for the Nordic syntaxa from association to alliance level. The diagnostic value of the different taxa is illustrated by the use of shadings and frames as suggested by BERG et al. (2001).

### 3.4.4. Phytosociological nomenclature

The naming of the syntaxa follows the International Code of Phytosociological Nomenclature (WEBER et al. 2000; referred to below as ICPN). For the treated associations, we list the synonyms (if necessary, with an indication of the relevant ICPN Article according to which they are invalid or illegitimate) and other names of similar content (for details of the presentation, see DENGLER et al. 2003). For the discussion of nomenclatural problems and reasons for the mentioned proposals to the Nomenclature Commission, see DENGLER & LÖBEL (2006). We have refrained from establishing formal subassociations and have used informal subtypes instead. We have checked the sources for the author citations of all syntaxa cited in the syntaxonomic overview (4.2) and the nomenclature paragraphs of section 5 and have included them in the reference list.

## 4. Classification

### 4.1. Placing the results into a syntaxonomic classification scheme

Historically, the basiphilous dry grasslands of shallow, skeletal soils were mostly regarded as part of the class *Festuco-Brometea* (e.g. ALBERTSON 1946). BRAUN-BLANQUET (1963) proposed placing the alvar communities rich in *Globularia vulgaris* into the new alliance *Helianthemo-Globularion* included in the continental order *Festucetalia valesiaceae* Br.-Bl. & Tx. ex Br.-Bl. 1950 of the class *Festuco-Brometea*, whereas he subordinated very open moss-rich stands ('*Schistidium apocarpum-Sedum album-Initiale*') to the *Sedo-Scleranthion* Br.-Bl. 1955. However, KRAHULEC et al. (1986) and DENGLER et al. (2003) pointed out that the large plots used by BRAUN-BLANQUET for the description of the *Helianthemo-Globularion* Br.-Bl. 1963 probably comprised a mixture of the two major types that already had been distinguished by ALBERTSON (1946, 1950), i.e. the '*Festucetum*' and the '*Avenetum*'. ROYER (1991), in his global synthesis of the *Festuco-Brometea*, nevertheless adopted BRAUN-BLANQUET's concept of the *Helianthemo-Globularion*, and was recently followed by RODWELL et al. (2002). However, an increasing number of authors agree that the vegetation types treated in our study belong as a whole to the dry grassland communities of shallow, skeletal soils within the class *Koelerio-Corynephoretea* (*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, DIERBEN 1996). This delimitation of the two classes was supported by the numerical analyses of BENGSSON et al. (1988) and our own studies (cf. LÖBEL 2002, LÖBEL & DENGLER subm.).

Dry grasslands of shallow skeletal soils are regarded as a class of their own by some authors (e.g. JULVE 1993, SCHAMINÉE et al. 1996b, RIVAS-MARTÍNEZ 2002) whereas others treat them as one order within the *Koelerio-Corynephoretea* (*Sedo-Scleranthetea*; e.g. KORNECK 1978, POTT 1995, DIERBEN 1996, SCHUBERT et al. 2001). From the level of order upwards, we follow the suggestions of DENGLER (2001, 2003: 201, 2004a) and DENGLER et al. (2003). Taken together, these communities are thus treated as subclass *Sedo-Scleranthenea* within the *Koelerio-Corynephoretea* and subdivided into an acidophytic order *Sedo-Scleranthetalia* and a basiphytic order *Alysso-Sedetalia*, each of which comprises more than one alliance at the European scale (see also MUCINA & KOLBEK 1993, RIVAS-MARTÍNEZ 2002).

HALLBERG (1971) pointed out that the Nordic *Alysso-Sedetalia* communities are quite distinct from their southern counterparts and suggested for them a provisional alliance, *Tortello-Sedion*, as counterpart to the southern *Alysso-Sedion*. This proposal was not followed by subsequent authors. The cluster analyses and ordinations of DENGLER & LÖBEL (2006), comprising numerous relevés from northern and central Europe, however, fully supported the concept of HALLBERG. DENGLER & LÖBEL (2006) thus validated his alliance, which has a considerable number of character and differential species, whereas the *Alysso-Sedion* proved to be mainly negatively characterised. With the inclusion of the Estonian relevés, the picture essentially remained the same (Fig. 1). The Nordic alliance *Tortello-Sedion* is characterised by the cryptogams *Ditrichum flexicaule*, *Cladonia pocillum*, *Distichium capillaceum*, *Bacidia bagliettoana*, *Encalypta rhaptocarpa* and *Tortella fragilis* which are also found in central Europe but are obviously much rarer in the *Alysso-Sedion* (DENGLER & LÖBEL 2006). The numerous differential taxa of the *Tortello-Sedion* (see DENGLER & LÖBEL 2006) 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 (*Agrostis stolonifera*, *Sagina nodosa*) can be highlighted. Within the Nordic communities, DENGLER & LÖBEL (2006) found a clear floristic dividing line corresponding to non-alvar sites and alvars, the latter distinguished by a large number of alvar-specific (and in part endemic) taxa (see also the differential species block in the Table 84 of DIERBEN 1996). This pattern is strengthened by the present study (Fig. 1, Table 3), and we thus accept these two units as suballiances, *Tortello tortuosae-Sedenion albi* and *Tortello rigentis-Helianthemion oelandici*, respectively (see 4.2).

DENGLER & LÖBEL (2006) accepted six associations within these two suballiances, which we could confirm in the present study (Table 3, see 4.2). Even the diagnostic taxa remain nearly unaltered, irrespective of the addition of 73 Estonian relevés. The communities of Saaremaa proved to belong to three associations of this system. In northern Europe outside the alvar areas (*Tortello-Sedenion*), we distinguish two associations. The relevés of HALLBERG (1971) as a whole occupy a quite distinct position within the classification. However, the types separated by him as '*Sedo-Tortelletum*', *Ditricho-Sedetum* and *Arenaria serpyllifolia-Sedum acre* community cannot be accepted at the rank of associations as they lack character species of their own; instead, they correspond to the three subtypes of our *Ditricho-Sedetum* s. l. (see 5.2). All other relevés from the Nordic countries outside the alvar regions, which have been published under different names (see 4.2), have to be placed in the somewhat heterogeneous central association *Cladonio-Sedetum* according to the principles pointed out in section 3.4.1. For the alvar sites (*Tortello-Helianthemion*), our classification shows many resemblances with former proposals dealing with the communities of Öland's Great Alvar (see nomenclature paragraphs of section 5). Already ALBERTSON's (1950) more detailed classification (aside from the simple *Sedetum-Festucetum-Avenetum* scheme adopted by many later authors) more or less corresponds to our units and the associations provisionally established by KRAHULEC et al. (1986) are even more similar to ours, which is why DENGLER & LÖBEL (2006) took up their names. In addition to the communities of

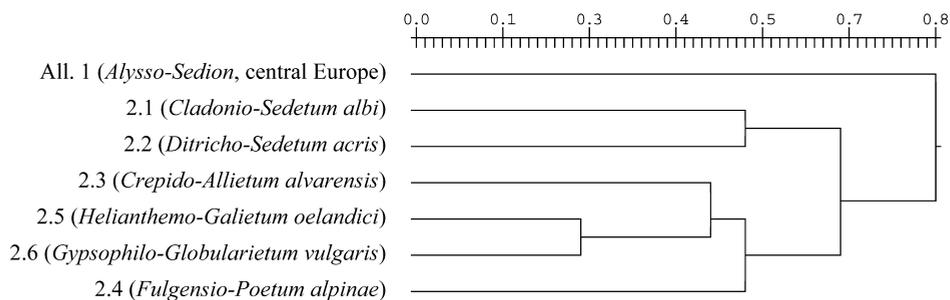


Fig. 1: Dendrogram for the Nordic associations and the central European alliance of the order *Alysso-Sedetalia*, based on the Bray-Curtis distance measure, a 'standardised' derivative of the Sørensen index (QUINN & KEOUGH 2002), applicable to percentage presence degrees. The agglomeration was done after the assignment of the relevés to the syntaxa and according to complete linkage; however, average and single linkage yielded the same results.

Abb. 1: Dendrogramm der nordischen Assoziationen und des mitteleuropäischen Verbandes der *Alysso-Sedetalia*. Die Clusteranalyse erfolgte mit dem Bray-Curtis-Distanzmaß, einer standardisierten Version des Sørensen-Indexes (QUINN & KEOUGH 2002), die sich auf prozentuale Stetigkeitslisten anwenden lässt. Die Agglomeration erfolgte nach der Zuordnung der Aufnahmen zu den Syntaxa mittels der complete linkage-Methode (average linkage und single linkage erbrachten das gleiche Ergebnis).

KRAHULEC et al. (1986), we separate the *Fulgensio-Poetum* as a fourth alvar association with many diagnostic species (see Fig. 1, Table 3). They did not distinguish it at association level from the *Crepido-Allietum*, though their numerical analyses also indicated two clusters (1A, approximately identical with the *Crepido-Allietum* s.str., and 1B, partly with the *Fulgensio-Poetum*). In the subsequent study of BENGTTSSON et al. (1988), the *Fulgensio-Poetum* was more clearly separated; their cluster 6 largely corresponds to our association.

As the relevés used in our analyses show a considerable nestedness, with some regions represented rather well and others not at all, one may argue that our classification could be distorted. Of course, it cannot be ruled out that the diagnostic value assigned to some of the species may be an artifact of spatial autocorrelation and thus further studies are desirable that more evenly include all Nordic regions. However, for both the large number of character and differential species and the fact that the addition of the Estonian records only lead to insignificant changes compared with DENGLER & LÖBEL (2006), even then, the classification system proposed in section 4.2 will probably prove valid in essence.

#### 4.2. Syntaxonomic overview of the treated syntaxa

The original diagnoses (= protologues) of the named new syntaxa according to the ICPN are included in DENGLER & LÖBEL (2006), which is supposed to be published approximately at the same time as the paper on hand.

Class: *Koelerio-Corynephoretea* Klika in Klika & Novák 1941 – Dry grasslands of sandy and shallow, skeletal soils

Subclass: *Koelerio-Corynephorenea* (Klika in Klika & Novák 1941) Dengler in Dengler et al. 2003 – Dry grasslands of sandy soils

Subclass: *Sedo-Scleranthenea* (Br.-Bl. 1955) Dengler in Dengler et al. 2003 – Dry grasslands of shallow, skeletal soils

Order: *Sedo-Scleranthetalia* Br.-Bl. 1955 – Acidophilous dry grasslands of shallow, skeletal soils

Order: *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 [central alliance]

All. 2: *Tortello tortuosae-Sedion albi* Hallberg ex Dengler & Löbel 2006 – Hemiboreal zone

- Suball. a: *Tortello tortuosae-Sedenion albi* (Hallberg ex Dengler & Löbel 2006) Dengler & Löbel 2006 – Non-alvar sites [central suballiance]  
 Assoc. 1: *Cladonio symphyrcarpiae-Sedetum albi* Tx. 1951 nom. invers. propos. [central association]  
 Assoc. 2: *Ditricho flexicaulis-Sedetum acris* Hallberg 1971
- Suball. b: *Tortello rigentis-Helianthemion oelandici* Dengler & Löbel 2006 – Alvar sites  
 Assoc. 3: *Crepido pumilae-Allietum alvarensis* Krahulec et al. ex Dengler & Löbel 2006  
 Assoc. 4: *Fulgensio bracteatae-Poetum alpinae* (Albertson 1950) Dengler & Löbel 2006  
 Assoc. 5: *Helianthemo oelandici-Galietum oelandici* Krahulec et al. ex Dengler & Löbel 2006 [central association]  
 Assoc. 6: *Gypsophilo fastigiatae-Globularietum vulgaris* Krahulec et al. ex Dengler & Löbel 2006

#### 4.3. Syntaxa of unclear position or of uncertain occurrence

Given the predominance of acidic soils in the Nordic countries (see 2.1), we should expect primarily communities of the acidophytic order *Sedo-Scleranthetalia* to occur there. However, there are only a few hints of such communities and no suitable relevés to be found in the literature. JALAS (1950), FREMSTAD (1997: unit F3c) and TYLER (1996), for example, mention stands with *Silene rupestris* which may be included in this order. The distribution and taxonomic position of *Sedo-Scleranthetalia* communities in northern Europe should therefore be a subject for future research. Some authors additionally place *Sedum anglicum* communities within the *Sedo-Scleranthetalia* (e.g. JULVE 1993, RIVAS-MARTÍNEZ 2002, RODWELL et al. 2002); however, we agree with DIERBEN (1996) that they are better included in the *Thero-Airion* Tx. ex Oberd. 1957 (*Koelerio-Corynephorenea*).

In this study, we have not considered the arctic-alpine alliance *Veronico-Poion glaucae* Nordhagen 1943, which is included in the *Alysso-Sedetalia* by DIERBEN (1996). According to the synoptic table presented by DIERBEN (1996: Table 71), the floristic relationships of the *Veronico-Poion* with the *Alysso-Sedetalia* are very weak: Character taxa of the order or the subclass are completely absent, and only two character species of the class occur in some of the subordinated units (*Ceratodon purpureus*, *Polytrichum piliferum*). This alliance perhaps might be placed as a separate order '*Sedo-Poetalia glaucae*' within the *Koelerio-Corynephoretea*, as suggested by RODWELL et al. (2002).

DIERBEN (1996) described the *Androsaco-Astragaletum alpini* Dierßen 1996 nom. inval., based on relevés of KLEIVEN (1959) from the northern Gudbrandsdalen in Norway. They contain a large number of typical *Alysso-Sedetalia* cryptogams, but due to their small size (0.25–1 m<sup>2</sup>) we did not consider them in this study (see 3.3). Some of the stands are dominated by grasses (e.g. *Festuca ovina*, *F. rubra*, *Poa angustifolia*) and could therefore be better placed in the *Trifolio arvensis-Festucetalia ovinae* Moravec 1967 (*Koelerio-Corynephorenea*). However, the stands particularly rich in typical cryptogams, therophytes (e.g. *Acinos arvensis*, *Androsace septentrionalis*) and stonecrops (*Sedum* spp.) probably belong to the *Tortello-Sedenion*. Whether they should be included in the central association *Cladonio-Sedetum* (see 5.1) or distinguished as a separate association (possibly characterised by terricolous lichens such as *Buellia epigaea*, *Rinodina* spp.), should be evaluated on the basis of larger, uniform-sized relevés from a greater area.

## 5. Characterisation of the associations

### 5.1. *Cladonio symphy carpiae-Sedetum albi* Tx. 1951 nom. invers. propos. (Table 4)

#### Nomenclature:

- Syn.: Festuco ovinae-Sedetum acris Vilberg 1927 nom. dub. p. max. p.  
 Sedetum tortellosum Albertson 1946 p. min. p. [Art. 3e]  
*Thymus serpyllum-Galium verum-Ditrichum flexicaule* assotsiatsioon sensu Laasimer 1965 p. p. [Art. 7, 34c]  
 Poo alpinae-Anthyllidetum ['Anthyllisetum'] vulnerariae Marker 1969 p. p. [syntax. syn.]  
 Sedetum acris Marker 1969 [syntax. syn.]  
 Alyso alyssoidis-Sedetum albi sensu Dengler & Rixen 1995, non Oberd. & T. Müller in T. Müller 1961  
 Ditricho-Thymetum sensu Paal 1998 p. max. p. [Art. 5, 7]  
 ? Androsaco-Astragaletum alpini ['(Kleiven 1959)'] Dierßen 1996 p. p. [Art. 5, 7]  
 Incl.: *Androsace septentrionalis-Sedum album*-[Tortello-Sedion]-Gesellschaft sensu Löbel 2002  
 Clusters 4 and 5 p. min. p. sensu Pärtel et al. 1999a  
 Note: Contrary to the suggestion of DENGLER & LÖBEL (2006), the epithet '*symphy carpiae*' does not need to be changed into '*symphy carpaee*' in the association name if one were to follow SANTESSON et al. (2004) as we do in the paper on hand, who regard *symphy carpia* as the correct spelling of the species epithet. The name *Festuco ovinae-Sedetum acris* ('*Festuca ovina-Sedum acre*-assotsiatsioon') of VILBERG (1927: 53) should be rejected according to Art. 37 ICPN since the author did not record cryptogams and thus the assignment of his relevés to the associations of the presented system is fraught with uncertainty.

**Floristic composition:** The *Cladonio-Sedetum* comprises poorly characterised stands dominated by *Sedum acre* or *S. album*. The vascular plants, among them several therophytes such as *Saxifraga tridactylites* and *Erophila verna*, grow mostly on moss cushions often dominated by *Tortula ruralis* agg. Many of the alvar-specific cryptogams are absent, unlike more acidophilous species such as *Ceratodon purpureus* and *Cerastium semidecandrum* which are present. *Brachythecium albicans*, *Allium oleraceum* and *Dactylis glomerata* differentiate the association from the others in the alliance. The community generally occurs in 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 5.4) of the Ölandic alvar. With an average of 'only' 29 terricolous taxa per 4 m<sup>2</sup>, the *Cladonio-Sedetum* shows the lowest phytodiversity of all the Nordic *Alyso-Sedetalia* communities.

**Ecology:** The *Cladonio-Sedetum* thrives in a range of different habitats, both natural and anthropogenic. In Norway, MARKER (1969) recorded the community from bare rocks or shallow soils over shell deposits and limestone bedrock (rel. J04–14, J30 and J31 of Table 4). On Öland, it is found on shore ridges in the north (DENGLER & RIXEN 1995; rel. J31 and J32 of Table 4), and rarely on rather atypical alvar sites in the south. On Saaremaa, the *Cladonio-Sedetum* grows on cliff tops and shore ridges but more often inhabits anthropogenic sites such as stone embankments, quarries, gravel deposits and concrete slabs found in industrial sites and former military training areas. The soil layer of the *Cladonio-Sedetum* is very thin or the substratum consists even completely of thick limestone gravel deposits with nearly no fine soil in between.

**Distribution:** The *Cladonio-Sedetum* as central association of the suballiance *Tortello-Sedion* is probably the most widely distributed association of the Nordic *Alyso-Sedetalia* communities. We expect it to occur in all areas where base-rich bedrock comes close to the surface in the southern parts of northern Europe and to reach the farthest northwards of the six associations. On Öland, it grows both in the north and the south but is rather rare and avoids well-developed alvar sites. In the Swedish province of Uppland, where the association was originally described from the small Baltic island of Runmarö (TÜXEN 1951; rel. J29 of Table 4), it had previously been documented by ALMQUIST (1929) under the name 'Succulent- och terofytsamhällen' as a widespread type. Some of the numerous records of the '*Sedetum tortellosum*' reported by ALBERTSON (1946) from the little alvar area of Kinnekulle

(Swedish mainland: Västergötland) that lack the alvar-typical cryptogams but have differential taxa of the first suballiance (*Ceratodon purpureus*, *Cladonia furcata*, *Cerastium semidecandrum*) can possibly also be included in the *Cladonio-Sedetum*. However, a definitive decision is impossible at present, since ALBERTSON (1946) used too small of plot sizes for it to be possible to compare his records with those included in our study. In Norway, the community occurs in the Oslofjord (MARKER 1969: rel. J04–14, J30 and J31 of Table 4, HALVORSEN 1980: blocks I–III), and according to the species lists in FREMSTAD (1997: units F3a and F3b) also in the Trondheimfjord. A part of the relevés of KLEIVEN (1959) from the northern Gudbrandsdalen (province of Oppland) assigned to the ‘*Androsaco-Astragaletum alpini*’ by DIERSEN (1996; see 4.3) probably also could be included in the *Cladonio-Sedetum*. In Estonia, the association is documented from the islands of Saaremaa (this paper, PÄRTEL et al. 1999a) and Hiiumaa (PÄRTEL et al. 1999a) as well as from the NW coast (PÄRTEL et al. 1999a) and the NE coast of the mainland (VILBERG 1927). From Finland, JALAS (1950) published some relevés from the southern provinces of Åland, Varsinais-Suomi, Uusimaa and Etelä-Häme that probably belong here as well.

**Subdivision:** We distinguish two geographic races. The one from Norway and the Swedish mainland (A) is differentiated by the arctic-alpine *Poa alpina* as well as *Allium oleraceum*, *Cladonia symphyocarpia* and some other taxa. The second geographic race (B), so far documented from Öland and Saaremaa, on the other hand, is distinguished by species such as *Medicago lupulina*, *Brachythecium albicans* and *Erophila verna*. Within this eastern race, there are two subtypes. The typical subtype (Ba) inhabits deeper soils with differential species such as *Dactylis glomerata* and *Achillea millefolium* indicating somewhat more mesic site conditions, and others, as *Artemisia campestris* and *Poa compressa*, exhibiting an affiliation to the western race. We found it at the cliff of Kaugatuma (peninsula of Sörve, rel. SBK01–03) but the majority of relevés originate from secondary habitats. By contrast, the *Hieracium pilosella* subtype (Bb) is found at sites very poor in fine soil and thus severely subject to summer drought. This is probably the reason why therophytes (*Hornungia petraea*, *Androsace septentrionalis*, *Thlaspi perfoliatum*) are here more important than in the other subunits. The relevés stem from shore ridges in northwest Saaremaa and from the small island of Vilsandi that lies about 3 km west of Saaremaa.

## 5.2. *Ditricho flexicaulis-Sedetum acris* Hallberg 1971 (Table 3: Assoc. 2)

### Nomenclature:

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

Incl.: *Arenaria serpyllifolia-Sedum acre*-[Sedo-Scleranthetea]-Gesellschaft sensu Hallberg 1971

*Ditrichum flexicaule*-[Sedo-Scleranthetea]-Gesellschaft sensu Hallberg 1971

Non: *Arenario serpyllifolii-Sedetum acris* Hallberg ex Passarge 1977 (= *Poo compressae-Saxifragetum tridactylitae* Géhu 1961)

**Floristic composition:** We describe the association here without presenting a vegetation table because only the already published relevés of the four named vegetation types of HALLBERG (1971) were available. The association is characterised by a very special cryptogam flora, including *Bacidia bagliettoana*, *Catapyrenium cinereum*, and *Tortella fragilis*, 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 grows close to the sea coast and thus hosts some ‘maritime’ taxa such as *Armeria maritima* subsp. *maritima*, which differentiate it from the other communities of the alliance. Compared to these, the community also contains a considerable number of mesophilous species (e.g. *Festuca rubra*, *Achillea millefolium*, *Lotus corniculatus*). The average species density on 4 m<sup>2</sup> is 41 and thus 40 % higher than in the *Cladonio-Sedetum*.

**Ecology:** In contrast to the *Cladonio-Sedetum* (see 5.1) the *Ditricho-Sedetum* does not occur on limestone but on acidic rocks covered by shallow soils or even on siliceous sand and gravel deposits which are secondarily enriched with base-rich material from shell deposits

(HALLBERG 1971). The community sometimes even grows close to the beach line, where some nutrient enrichment 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).

**Distribution:** All relevés included here originate from Bohuslän on the Swedish west coast (HALLBERG 1971). Few indications of phytocoenoses similar to the *Ditricho-Sedetum* of Bohuslän were available from other regions. However, we consider it possible 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 suspected character species *Tortella fragilis*, from a small island in the Oslofjord. Species lists by PETERSSON (1958: p. 193 and Table 31) from Litorina shore ridges in southern Gotland also show some similarities with this community, including the character taxa *Bacidia bagliettoana* and *Catapyrenium cinereum*.

**Subdivision:** Our subdivision largely corresponds to the communities of HALLBERG (1971). Numerous acrocarpous bryophytes and terricolous crustose lichens as well as some annual vascular plants differentiate the *Tortella tortuosa-Acinosa arvensis* subtype (a). It can be further divided into an *Agrostis vinealis* variant (a.1) and a *Lotus corniculatus* variant (a.2). The *Agrostis vinealis* variant (a.1) largely corresponds to the 'Sedo-Tortelletum' as delimited by HALLBERG (1971). Other differentiating species are *Homalothecium sericeum*, *Sagina nodosa* and *Sedum album*, the latter often dominating the herb layer. This variant inhabits shallow soils over rocks. The *Lotus corniculatus* variant (a.2) corresponds essentially to the *Ditricho-Sedetum* in the much narrower delimitation given in its original diagnosis by HALLBERG (1971) plus his *Ditrichum flexicaule* community. In addition to the name-giving species, it is also differentiated by *Bryum argenteum*, *Campanula rotundifolia* and some fruticose lichens. *Ditrichum flexicaule* is often the dominant component in its cryptogam layer. The variant a.2 occurs on gravel deposits with shells on less exposed sites, mainly on northern and eastern slopes. Finally, the *Carex caryophylla-Bromus hordeaceus* subtype (b) is equivalent to the *Arenaria serpyllifolia-Sedum acre* community of HALLBERG (1971). Within the association it shows the highest herb cover and inhabits the sites least affected by drought stress. This is expressed by the occurrence of several mesophilous differential taxa, amongst them graminoids such as *Bromus hordeaceus*, *Poa pratensis* agg., *Carex caryophylla*, and *Luzula campestris*. According to HALLBERG (1971), this subtype grows on sandy soils mixed with shells, situated further away from the beach line than is the case with the first subtype.

### 5.3. *Crepido pumilae-Allietum alvarensis* Krahulec et al. ex Dengler & Löbel 2006 (Table 5)

#### Nomenclature:

- Syn.: Festucetum tortellosum Albertson 1946 p. min. p. [Art. 3e]  
 Festucetum alvarense tortellosum Albertson 1950 p. p. [Art. 3e, 34a]  
*Festuca ovina-E rubra* v. *oelandica-Tortella tortuosa*-Ass. sensu Albertson 1950 p. p. [Art. 34c]  
 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 alvarense Krahulec et al. 1986 p. p. [Art. 3b, 34a]
- Incl.: *Agrostis stolonifera-Schistidium apocarpum*-Soziation sensu Albertson 1950  
*Artemisia rupestris* variant of the Carici flaccae-Seslerietum Paal 1998 nom. inval. [Art. 5, 7]  
 p. max. p.  
*Artemisia rupestris* variant of the Festucetum rubrae nom. illeg. [Art. 31] sensu Rebasoo 1975  
 p. max. p.  
*Festuca ovina-Hypnum bambergeri*-Soziation sensu Albertson 1950  
*Festuca ovina-Schistidium apocarpum*-Soziation sensu Albertson 1950  
 Clusters 6 p. min. p., 7 p. p. and 8 p. max. p. sensu Bengtsson et al. 1988  
 Cluster 6 sensu Pärtel et al. 1999a p. max. p.

**Floristic composition:** This community shows a peculiar mixture of xerophilous and hygrophilous elements. It is characterised by the continentally distributed *Artemisia*

*rupestris*. The name-giving taxa, *Crepis tectorum* subsp. *pumila* and *Allium schoenoprasum* var. *alvarense*, reach high presence degrees though they do not meet the character species criterion. The herb layer of the *Crepido-Allietum* is relatively dense and is dominated by the graminoids *Agrostis stolonifera*, *Festuca ovina*, and – on Öland – also *F. oelandica*. Several taxa indicating loamy soils such as *Leontodon autumnalis*, *Prunella vulgaris* and *Sagina nodosa* differentiate the association. In addition to typical *Tortello-Helianthemion* species, 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 *Chaenorhinum minus*, *Convolvulus arvensis*, and *Linaria vulgaris*.

**Ecology:** The community occurs on loamy or silty soils with an average depth of 7 cm, being the deepest amongst the *Tortello-Helianthemion* communities (DENGLER & LÖBEL 2006). Soils are often poorly drained and are affected by frost movements due to repeated freezing and thawing. This leads to polygon structures with sorted material or, more often, to soil hummocks which may be intensified by trampling cattle (e.g. STERNER & LUNDQVIST 1986). In contrast to the *Fulgensio-Poetum* (5.4), the bedrock is seldom exposed (mean cover: 6 %). The opposing forces of drought in summer and waterlogging in winter together with the mechanical stress of frost action explain the special species combination.

**Distribution:** In general, we expect this association to occur only in extreme alvar areas on poorly drained soils. On Öland, the community occurs both on the Great Alvar and in the smaller alvar areas on the east coast. One record of a stand dominated by *Artemisia rupestris* from the small island of Stora Karlsö near Gotland by WESTHOFF et al. (1983; rel. J33 of Table 5) can be placed in the association, although it exhibits more than three times lower species density than our relevés; this may be due to an incomplete species list. We know of no relevé from Gotland itself, though *Artemisia rupestris* occurs there (two unpublished relevés with this species by N. Ingerpuu belong to the class *Festuco-Brometea*). ALBERTSON (1946) described a periodically inundated ‘*Festuca-Tortella-Schistidium*-subassociation’ of his ‘*Festucetum tortellosum*’ from the alvar area of Kinnekulle (Västergötland). Although *Crepis tectorum* subsp. *pumila* and *Artemisia rupestris* are missing there, the stands may be included in the *Crepido-Allietum* through differential species such as *Prunella vulgaris*, *Sagina nodosa* and *Leontodon autumnalis*. On Saaremaa, the *Crepido-Allietum* is restricted to very open alvar areas that are found in the western part of the island and close to Ipla, north-east of Kuressaare. PAAL (1998) and PÄRTEL et al. (1999a) also mention it from the island of Hiiumaa. Whether stands rich in *Allium schoenoprasum*, *Crepis tectorum* and *Sagina nodosa* reported by VILBERG (1927) from NE Estonia and KROHN (1932) from small rocky islands southeast of Helsinki (Finland) also belong to this association is unclear, since these authors only presented species lists without cryptogams and did not discriminate infraspecific taxa.

**Subdivision:** We distinguish two geographic races. The first one (A) occurs on Öland and Gotland and is differentiated first and foremost by alvar-typical acrocarpous mosses (e.g. *Bryum elegans*, *Tortella rigens*, *Trichostomum crispulum*) that are generally rare or missing on Saaremaa. *Prunella vulgaris* and two pleurocarpous mosses of basiphilous fens (*Scorpidium turgescens*, *Drepanocladus cossonii*) are also concentrated in race A. This race can be further divided into two subtypes: The *Festuca oelandica*-subtype (Aa) is widely distributed on the Great Alvar of Öland. With an average of 36 terricolous taxa on 4 m<sup>2</sup> it is relatively species poor and inhabits sites most heavily affected both by inundation and frost movement. The mesophilous subtype (Ab), which on Öland mainly occurs in the smaller alvar areas on the east coast transitions into the communities of the *Festuco-Brometea* and the *Molinio-Arrhenatheretea* Tx. 1937. This is indicated by the high presence degrees of differential species such as *Plantago lanceolata*, *Homalothecium lutescens*, *Trifolium repens* and *Bromus hordeaceus*. The areas are grazed relatively intensively, mainly by cattle, and show extreme soil hummocks which can reach up to 30 cm in height. The sole relevé from Stora Karlsö (province Gotland; rel. J33 of Table 5) also belongs to this subtype. The geographic race of Saaremaa (B) shares a number of mesophilous taxa with subtype Ab of the western race (*Galium verum*, *Plantago lanceolata*, *Achillea millefolium*, *Medicago lupulina*) but also

has a great number of unique differential species. These are however hard to interpret as they cannot easily be assigned to one or a few ecological, sociological or chorological species groups. In some cases, alvar-typical taxa seem simply to be replaced by their more widespread relatives in the eastern race (e.g. *Bryum elegans* by *B. argenteum*, *Cerastium pumilum* by *C. semidecandrum* and *Festuca oelandica* by *F. rubra*). In addition, the character species of the association, *Artemisia rupestris*, is much more frequent in the Estonian race. Within each of the three before mentioned subunits (Aa, Ab and B), two variants occur, a negatively characterised typical variant (Aa.1, Ab.1, B.1) and a *Fulgensia bracteata* variant (Aa.2, Ab.2, B.2). The latter are characterised by colourful terricolous crustose lichens (*Fulgensia bracteata*, *Toninia sedifolia*, *Psora decipiens*) and *Tortella fragilis*. Their stands have a more open herb layer (mean cover 50 % compared to 65 % in the typical variants) and support an overall species density about 20 % higher than in the typical variants. The sites are probably subject to a more severe disturbance regime than those of the typical variants, and thus the *Fulgensia bracteata* variants can be seen as pioneer stages.

#### 5.4. *Fulgensio bracteatae-Poetum alpinae* (Albertson 1950) Dengler & Löbel 2006 (Table 6)

##### Nomenclature:

Syn.: Sedetum tortellosum Albertson 1946 p. max. p. [Art. 3e]

*Sedum album-Tortella tortuosa-Cladonia symphyrcarpia*-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]

Crepidio-Allietum alvarensense Krahulec et al. 1986 p. p. [Art. 3b, 34a]

Incl.: *Sedum album-Tortella inclinata*-Soziation sensu Albertson 1950

*Fulgensia bracteata-Poa alpina*-[Tortello-Sedion]-Gesellschaft sensu Löbel 2002

Clusters 6 p. max. p. and 8 p. min. p. sensu Bengtsson et al. 1988

**Floristic composition:** With large moss cushions of *Ditrichum flexicaule* and *Tortella* species regularly spread over the otherwise nearly bare bedrock, the *Fulgensio-Poetum* is physiognomically quite distinct from all other communities. These cushions have heights of 5–10 cm and host most of the other species. The association is characterised by its rich cryptogam flora, especially the crustose lichens *Fulgensia bracteata*, *F. fulgens*, *Mycobilimbia lurida* and *Toninia sedifolia*. *Ceratodon conicus*, *Schistidium atrofusum* and *Tortella calcicolens* are characteristic moss species. Vascular plants are relatively unimportant for the community structure (mean cover 18 %). Among these, *Sedum album* attains the highest degree 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 of the suballiance.

**Ecology:** The community is the first vascular plant association to colonise bare rocks and extremely shallow soils. Thus it shows the highest cover of bare rock (mean: 28 %). During the succession, the small moss cushions grow together and accumulate more and more soil beneath. This 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 less affected by inundation and frost movements than the *Crepidio-Allietum* (5.3).

**Distribution:** On Öland, the community mainly grows in the Great Alvar but rarely also in some small alvar regions on the east coast. In addition to southern Öland, the *Fulgensio-Poetum* also occurs in a small alvar region on the northwest coast of this island. Only little information is available on the occurrence of the association on Gotland. The relevé of the ‘*Mollia tortuosa*-Therophyten-Ass.’ documented by DU RIETZ (1925) NE of Visby and some of the (incomplete?) species lists of PETERSSON (1958) probably belong to the *Fulgensio-Poetum*. More recently, OTT et al. (1996) also documented the association on Gotland but because of the small plot size, their relevés have not been included in the present study. Due to the high number of alvar-specific cryptogams found in the ground layer, most of the numerous records of the ‘*Sedetum tortellosum*’ reported by ALBERTSON (1946) from the

little alvar area of Kinnekulle (Swedish mainland: Västergötland) probably belong to the *Fulgensio-Poetum* (see also 5.1). On Saaremaa, the *Fulgensio-Poetum* is absent.

**Subdivision:** As the community is very homogenous in structure and composition, no subtypes are differentiated.

#### 5.5. *Helianthemo oelandici-Galietum oelandici* Krahulec et al. ex Dengler & Löbel 2006 (Table 7)

##### Nomenclature:

- Syn.: Sedo-Cetrarietum islandicae Du Rietz 1925 [Art. 3d (Principle II Paragraph 2)]  
 Festucetum tortellosum Albertson 1946 p. max. p. [Art. 3e]  
*Festuca ovina-Tortella inclinata-Cetraria islandica*-association Albertson 1946 [Art. 34c]  
 Festucetum alvarense cetrariosum Albertson 1950 [Art. 3e]  
 Festucetum alvarense tortellosum Albertson 1950 p. p. [Art. 3e, 34a]  
*Festuca ovina-F. rubra* v. *oelandica-Tortella tortuosa*-Ass. sensu Albertson 1950 p. p. [Art. 34c]  
*Helianthemum oelandicum-Festuca ovina-Cetraria islandica*-Ass. Albertson 1950 [Art. 34c]  
*Thymus serpyllum-Galium verum-Ditrichum flexicaule* assotsiatsioon sensu Laasimer 1965 p. p. [Art. 7, 34c]  
 Helianthemo-Galietum oelandici Krahulec et al. 1986 [Art. 3b]
- Incl.: *Helianthemum oelandicum-Festuca ovina-Tortella tortuosa*-Soziation sensu Albertson 1950  
*Schistidium apocarpum-Sedum album*-[Sedo-Scleranthion]-Initialgesellschaft sensu Br.-Bl. 1963  
 Clusters 5 p. p. and 7 p. p. sensu Bengtsson et al. 1988  
 Cluster 5 sensu Pärtel et al. 1999a p. max. p.

**Floristic composition:** The flowering aspect of the community is dominated by the dwarf shrubs *Thymus serpyllum* (widely distributed) and *Helianthemum oelandicum* subsp. *oelandicum* (only on Öland, jointly with the *Gypsophilo-Globularietum*, see 5.6). Floristically, this central association is poorly positively characterised. *Galium oelandicum* and *Sisymbrium supinum* are probably the sole character species, but they only gain low to intermediate presence degrees and are absent from parts of the distribution area. KRAHULEC et al. (1986) mention *Hieracium x dichotomum* as a further potential character species, but our own data do not support this. In the cryptogam layer, fruticose lichens, including *Cetraria aculeata*, *C. islandica* and *Cladonia foliacea*, play a comparably important role as in the *Gypsophilo-Globularietum* (see 5.6). Based on their overall species composition relevés from Gotland and Saaremaa are also included in the association although the name-giving species are absent there.

**Ecology:** On Öland, the community occurs on sites with significantly deeper soils (mean: 5.7 cm; DENGLER & LÖBEL 2006) than the *Fulgensio-Poetum* (section 5.4), probably following it in succession when the vegetation cover becomes more closed. On Saaremaa, it grows in alvar sites as on cliff tops and shore ridges. Ecologically, the community mediates between the *Crepido-Allietum* (5.3) and the *Gypsophilo-Globularietum* (5.6).

**Distribution:** In southern Öland, the community occurs all over the Great Alvar, often covering huge areas, but is rather rare in the small alvar areas along the east coast. Though the name-giving species are restricted to Öland, relevés from the other alvar regions can also be assigned to the *Helianthemo-Galietum* when this is conceived as a broadly delimited central association whose limits are primarily fixed by differential species groups. This holds true for the '*Sedum-Cetraria islandica*-Ass.' reported by DU RIETZ (1925; rel. J34–35 in Table 7) and some relevés by PETERSSON (1958) and OTT et al. (1996) from Gotland. Most of the relevés of the '*Festuca-Tortella-Cetraria*-subassociation' within the '*Festucetum tortellosum*' reported by ALBERTSON (1946) from the Kinnekulle alvar area on the Swedish mainland may be placed here as well. In Estonia, we found the association in the westernmost parts of Saaremaa and on the island of Vilsandi. Whether the relevés of VILBERG (1927: 86) from NE Estonia also belong to the *Helianthemo-Galietum* cannot be said with certainty as the author did not identify the diagnostically relevant lichens.

**Subdivision:** We distinguish two geographic races. The first (A) is known from Öland and Gotland. It is primarily differentiated by endemic taxa of these islands (*Helianthemum*

*oelandicum* subsp. *oelandicum*, *Allium schoenoprasum* var. *alvarense*), a number of therophytic vascular plants (e.g. *Hornungia petraea*, *Cerastium pumilum*) and some arctic-alpine lichens (*Thamnolia vermicularis*, *Flavocetraria nivalis*). Within this race, there are two subtypes. The *Didymodon fallax-Distichium capillaceum* subtype (Aa) is differentiated first and foremost by small, mostly acrocarpous mosses (besides the name-giving species, e.g., *Trichostomum crispulum*, *Pleuroidium acuminatum*, *Tortella rigens*). With an average of 54 terricolous taxa on 4 m<sup>2</sup>, this subtype is exceptionally species-rich. The *Cladonia furcata-Sedum rupestre* subtype (Ab), on the other hand, is differentiated by perennial vascular plants and fruticose lichens but has distinctly lower species densities. The two subtypes differ also in mean vegetation cover (herb layer: 44 % vs. 66 %; cryptogam layer: 33 % vs. 52 %) and soil pH (7.4 vs. 6.8). Obviously, the sites inhabited by subtype Aa are subject to more severe frost movements than those of subtype Ab. The Estonian race (B) is mainly negatively characterised, though some mesophilous taxa show increased frequencies here (e.g. *Centaurea jacea*, *Achillea millefolium*); some of these taxa are shared with the *Cladonia furcata-Sedum rupestre* subtype of the western race (e.g. *Avenula pratensis*). As in the *Crepidio-Allietum* (see 5.3), two variants are distinguishable within each of the named three major subunits (Aa, Ab, B), namely a typical variant and a *Fulgensia bracteata* variant. The latter variants (Aa.2, Ab.2, B.2) comprise the more open stands, and are richer in bryophyte and lichen species but poorer in vascular plants than the typical variants.

#### 5.6. *Gypsophilo fastigiatae-Globularietum vulgaris* Krahulec et al. ex Dengler & Löbel 2006 (Table 8)

##### Nomenclature:

- Syn.: *Avena pratensis-Sesleria coerulea-Camptothecium lutescens*-Ass. Albertson 1950 p. p. [Art. 34c]  
*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]  
 Incl.: *Globularia vulgaris*-Soziationen sensu Albertson 1950  
 Clusters 4 and 5 p. p. sensu Bengtsson et al. 1988

**Floristic composition:** With an average of 52 terricolous species on 4 m<sup>2</sup>, the *Gypsophilo-Globularietum* is the *Alysso-Sedetalia* association with the highest species density in northern Europe. It 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*. Additionally, glabrous individuals of *Arabis hirsuta*, which are known from Öland and Gotland, 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). Other south-eastern plants differentiating the *Gypsophilo-Globularietum* from the *Helianthemo-Galietum* (5.5) are *Vincetoxicum hirundinaria*, *Melica ciliata* and *Oxytropis campestris*. On the other hand, the arctic-alpine lichens *Flavocetraria cucullata*, *F. nivalis*, and *Thamnolia vermicularis* are more prominent in the *Gypsophilo-Globularietum* than in any other community of the alliance. Species indicating moist soil conditions are absent; *Agrostis stolonifera* is replaced by *A. gigantea*. The cryptogam flora is in general quite similar to that of the *Helianthemo-Galietum* (5.5) but with *Rhytidium rugosum*, *Grimmia pulvinata* and *Cladonia convoluta* as differential species.

**Ecology:** On Öland, the community occurs on shallow soils, the depth of which varies due to many fissures in the limestone bedrock, especially in karst areas. 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 deeper rock fissures may prevent these sites from completely drying out in summer. The *Gypsophilo-Globularietum* normally covers relatively small areas which are interspersed with small groups of *Juniperus communis* shrubs colonising deeper fissures in the bedrock, especially when grazing intensity is low. Sites thus are often threatened by overgrowing.

**Distribution:** The association seems to be endemic to Öland, Gotland and Stora Karlsö. In southern Öland, the *Gypsophilo-Globularietum* occurs exclusively on the Great Alvar.

According to the distribution map of *Globularia vulgaris* by STERNER & LUNDQVIST (1986), it seems possible that the association also can be found in central and northern Öland. We have one relevé from Stora Karlsö, a small island near Gotland's coast (WESTHOFF et al. 1983; rel. J23 in Table 8), and PETERSSON (1958) presented some species lists (Tables 19A, 28 and 32) which also seem to belong to this association. However, further information about the Gotlandic alvar vegetation is required. In the other Nordic alvar regions (Kinnekulle and Estonia), *Globularia vulgaris* is absent as is the association. The few other geographically restricted occurrences of the second character species *Gypsophila fastigiata* in central Sweden and Finland (cf. MOSSBERG & STENBERG 2003) presumably do not belong to the *Gypsophila-Globularietum*.

**Subdivision:** We distinguish two subtypes: The common subtype (a) is rich in fruticose lichens. A typical (a.1) and a *Dicranum scoparium-Avenula pratensis* variant (a.2) can be distinguished. The first (a.1) inhabits relatively shallow soils and is differentiated by species such as *Melica ciliata* and *Hypogymnia physodes*. The second, more mesophilous variant (a.2) grows on deeper and more acidic soils. It is differentiated by species such as *Dicranum scoparium* and *Sedum rupestre* and typically exhibits a relatively high cover of *Avenula pratensis*. It transitions into communities of the *Festuco-Brometea*. The *Centaurea scabiosa* subtype (b), which is poor in fruticose lichens, occurs along the roads crossing the Great Alvar. It is distinguished by 'ruderal' species such as *Centaurea scabiosa* which are completely absent from the central parts of the Great Alvar but are quite common along the roads all over the island.

## 6. Discussion

### 6.1. Potential and limitations of the classification methodology

Although many authors in the past have elaborated on the peculiarities of different Nordic plant communities compared with their southern counterparts, only a few have proposed formalised syntaxa for them (e.g. BRAUN-BLANQUET 1963, HALLBERG 1971, KRAHULEC et al. 1986). There may have been both historical reasons for this (e.g. supraregional classification not being the main focus of the Uppsala school of vegetation science) and reasons rooted in the nature of the Nordic phytocoenoses themselves. On the one hand, Nordic phytocoenoses are often characterised by a mixture of taxa that in other geographic regions rarely occur together (e.g. DIERSCHKE 1974, DIEKMANN 1995, LÖBEL & DENGLER subm.). On the other hand, 'moving northwards in Europe, one observes a successive loss of species in general, and of diagnostic species in particular' (DIEKMANN 1995). This is especially true for deciduous forests, fringe communities and semi-dry grasslands. However, such a loss of diagnostic species does not occur in dry grassland communities of shallow, skeletal soils (DENGLER & LÖBEL 2006).

DIEKMANN (1995) made four suggestions for overcoming the resulting problems in the phytosociological classification of northern European plant communities: (1) regional associations, (2) restriction of character species to structural vegetation types, (3) the use of environmental information for the classification, and (4) the use of cryptogams.

Both (2) and (4) are also essential parts of the classification method of DENGLER (2003), which we have used in this study. The restriction of character species to *a priori* separated structural types (2) enabled us to use bryophytes and lichens as character species of a herbaceous plant community, irrespective of whether they are character taxa of pure cryptogam communities. Without this 'rule', it would probably have been impossible to recognise the *Fulgensio-Poetum*. Since we do not know of any proposal for the *a priori* delimitation of herbaceous against cryptogam communities, we had to apply a new definition (see 3.4.1), which, however, may be criticised. Cryptogams make up about one-half of the diagnostic species of all the taxonomic levels determined by us, which underlines their great relevance for classification (4).

The two other suggestions of DIEKMANN (1995), however, need critical revision: (1) to restrict the validity of character species geographically has been previously suggested by

BERGMEIER et al. (1990), DIERSCHKE (1992), and SCHUBERT (1995). DIEKMANN prefers the proposal of SCHUBERT, to use phytogeographically delimited regions such as the nemoral and the boreo-nemoral zones. However, this concept has two major flaws (cf. DENGLER 2003: 95): Firstly, vegetation scientists are far from a consensus as to which the relevant phytogeographical units are and where their borders run. Secondly, consistently applied, such an approach would lead to an enormous increase in the number of syntaxa, since no syntaxa spanning more than one of these geographic units separated *a priori* would be allowed. For this reason, the approach of the other authors (BERGMEIER et al. 1990, DIERSCHKE 1992, DENGLER 2003), who define the validity area of character species intrinsically by the range in which the next superior syntaxon is distributed, seems to be truer to the purpose. By applying this approach (see 3.4.1), we were able to establish some character species of Nordic *Tortello-Sedion* associations, despite the fact that they certainly grow in a different sociological context within their disjunct main distribution range (*Globularia vulgaris*, *Gypsophila fastigiata*, *Artemisia rupestris* and probably also some of the cryptogams; see 6.2). (3) The suggestion of DIEKMANN (1995) to use information on site conditions for the classification of syntaxa has to be rejected since this would be circular reasoning (cf. DENGLER 2003: 48).

Of equal or even higher importance than the points just discussed for the classification presented here is the application of the central syntaxon concept at all hierarchical levels (cf. DIERSCHKE 1981, DENGLER 2003: 103). Central syntaxa have no or too few character taxa of their own rank. This may reflect their ecological central position or their geographically marginal position in relation to their superior syntaxon (cf. DIERSCHKE 1981, 1994, DENGLER 2003). The *Alyso-Sedion* can thus be considered as a geographic central alliance of the order, and the *Helianthemo-Galietum* as an ecological central association of the suballiance, i.e. occupying the ecologically intermediate sites (see 5.5). A critical point concerning central syntaxa remains. Potentially they could be more heterogeneous than positively characterised syntaxa of the same rank. This problem, however, is minimised when classifying relevés according to their total species composition (as we did) and not only on the basis of the character species that occur.

To sum up, using the consistent approach just outlined (see 3.4.1), we were able to work out floristically well-delimited (see Table 3) and both ecologically (see DENGLER & LÖBEL 2006) and chorologically meaningful syntaxa (section 6.2) at all hierarchical levels. This confirms the positive experience gained with this approach by BERG et al. (2001, 2004).

## 6.2. Chorology and synchronology

The diagnostic species of the *Tortello-Sedion* and its subunits include several taxa with restricted distribution areas. Of these, *Helianthemum oelandicum* subsp. *oelandicum*, *Galium oelandicum* and *Crepis tectorum* subsp. *pumila* are assumed to be endemic to Öland, and *Allium schoenoprasum* var. *alvarense*, *Festuca oelandica*, *Hieracium x dichotomum* and *Silene uniflora* subsp. *petraea* are only known from Öland and Gotland (MOSSBERG & STENBERG 2003, JONSELL & KARLSSON 2004). On Saaremaa, however, we found plants morphologically closely resembling the Ölandic specimens of *Crepis tectorum* subsp. *pumila*, *Allium schoenoprasum* var. *alvarense* and *Festuca oelandica* growing in the corresponding communities (marked with 'cf.' in our tables). The two first-named had already been listed for this country by some Estonian authors (*Crepis*: LEHT 1999; *Allium*: EICHWALD et al. 1984) although JONSELL & KARLSSON (2004) still claim them as Swedish endemics. Systematic studies are needed to resolve the contrasting opinions. *Arenaria gothica*, a further probable character species of the suballiance (cf. ALBERTSON 1946, PETERSSON 1958), occurs only 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). However, we did not find it there. The characteristic

endemics are mostly infraspecific taxa or belong to closely related aggregates. This is not surprising, given that these taxa must be evolutionary quite young. Indeed, the entire distribution range of the Nordic *Alysso-Sedetalia* communities was covered by ice during the Weichselian glacial period. It is however remarkable that *Tortello-Sedion* obviously hosts more geographically narrowly restricted taxa than the *Alysso-Sedion* (cf. DENGLER & LÖBEL 2006), and also that a considerable part of the few strictly Nordic endemics (cf. JONSELL & KARLSSON 2004) occur only in such xerothermophilous ('southern') communities. The other characteristic vascular plants of the Nordic alvar communities are geographically separated outliers from their main distribution areas in south-western Europe (*Globularia vulgaris*, *Sisymbrium supinum*), (south-)eastern Europe (*Gypsophila fastigiata*) and central Asia (*Artemisia rupestris*; e.g. HULTÉN & FRIES 1986; cf. 6.1). As regards the diagnostic bryophytes and lichens (see Table 3), these are mostly geographically widespread but much rarer in temperate dry grasslands (DÜLL & MEINUNGER 1989, DÜLL 1994a, 1994b, WIRTH 1995, DIERBEN 2001) than in the Nordic communities, especially those of the alvars (cf. DENGLER & LÖBEL 2006). In the Mediterranean region, however, many of these species may be quite frequent again in sun-exposed communities of base-rich substrata (cf. DIERBEN 2001 and own observations) though a realistic assessment of their presence degrees in these syntaxa is not yet possible since even the most recent comprehensive studies of Mediterranean dry grasslands (e.g. PEÑAS et al. 2001, BIONDI et al. 2005) do not record cryptogams, despite their known ecological importance and diagnostic value.

As DENGLER & LÖBEL (2006) point out, the two distribution centres visible on the synchorological map of the *Sedo-Scleranthenea* by DENGLER (2003: 218) convincingly correspond to the two distinguished alliances, *Alysso-Sedion* in the mountainous regions of temperate Europe and *Tortello-Sedion* in the southern parts of Norway, Sweden and Finland plus Estonia. The range of the Nordic alliance also closely fits to the natural range of subclass character species *Sedum album* in the Nordic countries (MEUSEL et al. 1965). Most occurrences lie in the boreonemoral zone with only few outposts in the southern boreal zone (terminology after SJÖRS et al. 2004); the northernmost stands are indicated from the Trondheimsfjord (c. 64° N, cf. 5.1). The *Tortello-Sedion* obviously reaches its eastern limits in Estonia and Finland as species lists from dry grasslands of the Russian alvar sites in the St. Petersburg region do not include any *Alysso-Sedetalia* species (ZNAMENSKIY et al. in press). Within the Baltic countries, the *Tortello-Sedion* seems to be restricted to Estonia as the dolomite outcrop communities in Latvia lack the diagnostic species of the Nordic alliance (JERMĀCĀNE & LAIVIŅŠ 2001) and thus belong to the *Alysso-Sedion*. Whether the *Poo compressae-Saxifragetum tridactylitae* Géhu 1961 as widespread central-association of the *Alysso-Sedion* (cf. DENGLER 2004a) also reaches the southernmost parts of Sweden (limestone districts of Skåne or anthropogenic sites) is unknown as no relevés were available from there.

The known distribution of the six associations as outlined in section 4 is synoptically shown in the maps of Fig. 2. Classifying the relevés by their complete species combination and not only by their character species results in more broadly delimited associations. In such a wider circumscription, neither the *Crepido-Allietum* nor the *Helianthemo-Galietum* is endemic to Öland, as was supposed by KRAHULEC et al. (1986). Still, the suballiance *Tortello-Helianthemion* is restricted to the four alvar regions Västergötland, Öland, Gotland, and Estonia. All its four associations occur on Öland and, though lacking some diagnostic species, also on Gotland and the adjacent islands. The Kinnekulle alvar area on the Swedish mainland is inhabited by three of the alvar associations whereas in Estonia there are only two.

### 6.3. Plant diversity

With mean total species numbers per 4 m<sup>2</sup> between 32.4 (*Cladonio-Sedetum*) and 53.6 (*Gypsophilo-Globularietum*), the Nordic dry grassland communities of shallow, skeletal soils are exceptionally species-rich at small scales (see Table 3). Both on Öland and on Saaremaa, the communities of the *Tortello-Helianthemion* exceed the mean species densities of

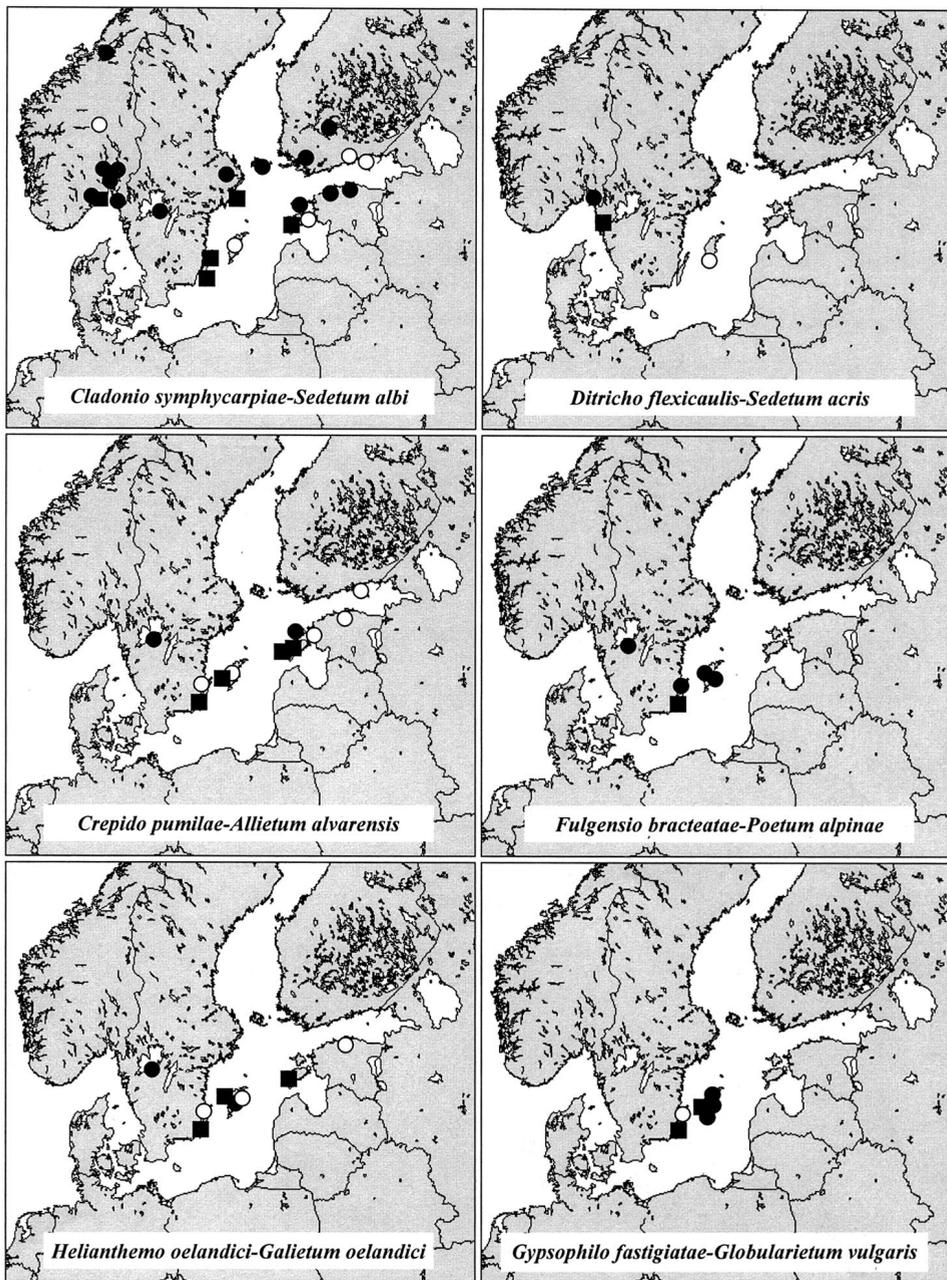


Fig. 2: Known distribution of the six associations of the *Tortello tortuosae-Sedion albi*. Full quadrats indicate certain occurrences, i.e. relevés included in this study. Full circles refer to probable and open circles to possible occurrences based on literature data.

Abb. 2: Bekannte Verbreitung der sechs Assoziationen des *Tortello tortuosae-Sedion albi*. Gefüllte Quadrate stehen für sichere Vorkommen, d. h. Aufnahmen die in unserer Klassifikation direkt berücksichtigt wurden. Gefüllte Kreise beziehen sich auf wahrscheinliche und offene Kreise auf mögliche Vorkommen basierend auf der ausgewerteten Literatur.

all other dry grassland associations (LÖBEL et al. 2004, BOCH & DENGLER 2006). The maximum value of 80 species (excluding saxicolous crustose lichens) per 4 m<sup>2</sup> recorded in the Ölandic *Gypsophilo-Globularietum* (see Table 8), is among the highest species densities on a small scale ever documented (DENGLER 2005). Only lichen-rich dwarf-shrub communities on Greenland (e.g. LÜNTERBUSCH & DANIËLS 2004: up to 83 species on 4 m<sup>2</sup>) and meadow steppes in Russia (e.g. DONIȚĂ et al. 2003: up to 80 species on 1 m<sup>2</sup>) are known to have a similar or higher species richness on this scale. BOCH (2005) also analysed 100 m<sup>2</sup> plots. For the Estonian stands of the *Crepido-Allietum*, he found a mean of 113.3 species and a maximum value of 140 species (including saxicolous crustose lichens), both counts being considerably beyond the highest known values for European dry grasslands listed in DENGLER (2005).

Each of the six *Tortello-Sedion* associations has significantly higher species densities than the central European *Alysso-Sedion* (mean: 17.7 species per 4 m<sup>2</sup>; DENGLER & LÖBEL 2006). Though the difference is most pronounced in bryophytes and lichens, it is still significant for vascular plants (DENGLER & LÖBEL 2006). Within the *Tortello-Sedion*, the alvar communities (*Tortello-Helianthemion*) are richer in bryophytes ( $p < 0.05$ ) and lichens ( $p < 0.05$  only for *Cladonio-Sedetum*) but poorer in vascular plants (n.s.) compared with the two associations of the widespread central suballiance *Tortello-Sedenion* (DENGLER & LÖBEL 2006). Comparing the three associations occurring both on Öland and on Saaremaa, we found no consistent trends in richness, the Ölandic stands being distinctly more diverse in the case of the *Cladonio-Sedetum* and the *Helianthemo-Galietum* but poorer in the *Crepido-Allietum*. However, if we exclude the *Festuca oelandica* subtype of the latter association, that has no counterpart on Saaremaa, this association also has higher species densities on Öland; the differences, however, are not significant. It may thus be concluded that the more 'alvar-like' the sites, the higher the small-scale species richness.

DENGLER & LÖBEL (2006) discuss the probable reasons for the outstanding diversity of *Tortello-Sedion* communities in general and of the alvar sites in particular. They propose a large species pool due to long-lasting habitat continuity, high spatio-temporal small-scale heterogeneity, reduced competition, and the small size of the individual plants as probable causes. When analysing the diversity patterns of all Ölandic dry grassland types, LÖBEL et al. (in press) found that species richness is positively related to soil pH and negatively to soil depth; thus *Tortello-Sedion* communities with the highest pH values and the most shallow soils of the studied communities are at the top. Additionally, they found that microtopography (leading to enhanced small-scale heterogeneity) is positively correlated with total species richness.

#### 6.4. Properties and syntaxonomic position of the *Tortello-Sedion* communities, compared with central Europe and related to other Nordic syntaxa

When we examine five higher syntaxa that are mainly distributed in the nemoral zone and reach their northern limits in the boreo-nemoral zone, common properties as well as interesting differences become evident (Table 9). (1) The Nordic communities show a peculiar mixture of species that rarely co-occur in central European stands. This has already been pointed out by DIERSCHKE (1974) and DIEKMANN (1995, 1997). In the southern part of northern Europe, species with oceanic, continental, arctic-alpine or submediterranean distributions, as well as species usually thought of as acidophytic or basiphytic and xerophytic or hygrophytic, may frequently grow intermingled in the same phytocoenosis. (2) The relative importance of bryophytes and lichens also increases generally in the Nordic communities compared to their central European counterparts. Interestingly, neither of these differences can be found in the *Koelerio-Coryneporena*. (3) Regarding the species pool, one should expect a decrease for the predominantly central European vegetation types when moving northwards. However, this pattern does not occur in the *Koelerio-Coryneporena*, and it is even reversed in the *Sedo-Scleranthenea*. In the latter subclass, this increase in the regional species pool size is caused both by a number of endemic taxa and by the relative abundance

Table 9: Comparison of the Nordic phytocoenoses of five (sub-)classes with their central European counterparts.

++ = much higher; + = higher; ± = similar; – = lower; symbols in brackets indicate slight and/or uncertain differences.

Major sources: *Sedo-Scleranthenea* (this paper), *Koelerio-Corynephoronea* (LÖBEL 2002, DENGLER 2004d, 2005, DENGLER et al. 2004), *Festuco-Brometea* (DIEKMANN 1997, JANDT 1999, LÖBEL 2002, DENGLER 2004d, 2005, DENGLER et al. 2004, BOCH & DENGLER 2006), *Trifolio-Geranietea* (DIERSCHKE 1974, DIEKMANN 1997, DENGLER & KREBS 2003, J. Dengler & S. Boch unpubl.), *Quercu-Fagetea* (DIEKMANN 1995).

Tab. 9: Vergleich der nordischen Gesellschaften von fünf (Unter-)Klassen mit ihren jeweiligen mitteleuropäischen Entsprechungen.

++ = viel höher; + = höher; ± = ähnlich; – = niedriger; eingeklammerte Symbole stehen für geringfügige bzw. unsichere Unterschiede.

Hauptquellen: *Sedo-Scleranthenea* (vorliegender Artikel), *Koelerio-Corynephoronea* (LÖBEL 2002, DENGLER 2004d, 2005, DENGLER et al. 2004), *Festuco-Brometea* (DIEKMANN 1997, JANDT 1999, LÖBEL 2002, DENGLER 2004d, 2005, DENGLER et al. 2004, BOCH & DENGLER 2006), *Trifolio-Geranietea* (DIERSCHKE 1974, DIEKMANN 1997, DENGLER & KREBS 2003, J. Dengler & S. Boch unpubl.), *Quercu-Fagetea* (DIEKMANN 1995).

	<i>Sedo-Scleranthenea</i>	<i>Koelerio-Corynephoronea</i>	<i>Festuco-Brometea</i>	<i>Trifolio-Geranietea</i>	<i>Quercu-Fagetea</i>
Peculiar species mixture	yes	no	yes	yes	yes
Species pool size	+	±	–	(–)	–
Species density	++	+	(+)	+	?
Proportion of cryptogams	++	±	+	+	+
Separate Nordic syntaxa	yes	no	yes	yes	yes

of taxa that only have scattered occurrences further south. (4) Contrary to intuition, species densities in all the Nordic syntaxa for which we have data are higher than in their southern equivalents (see 6.3).

Within the *Sedo-Scleranthenea*, the *Festuco-Brometea*, the *Trifolio-Geranietea sanguinei* T. Müller 1962 and the *Quercu-Fagetea* Br.-Bl. & Vlieger in Vlieger 1937, these four points together lead to quite distinct vegetation types inhabiting the boreo-nemoral zone. Interestingly, within the sandy dry grasslands (*Koelerio-Corynephoronea*), no separate Nordic alliance and not even an association seem to exist (LÖBEL 2002, BOCH & DENGLER 2006, LÖBEL & DENGLER subm.). Recently, separate Nordic alliances comparable to the *Tortello-Sedion* have also been proposed for the basiphilous semi-dry grasslands (DENGLER et al. 2003: 607, DENGLER 2004b: *Filipendulo vulgaris-Helictotrichion pratensis* Dengler & Löbel in Dengler et al. 2003) and the xerothermic fringe communities (DENGLER & KREBS 2003, DENGLER 2004c: *Galio littoralis-Geranium sanguinei* Géhu & Géhu-Franck in de Foucault et al. 1983). DIEKMANN (1994, 1995) showed the distinctness of the deciduous forest communities of southern Scandinavia compared with the central European types, but a formal phytosociological classification of them has not yet been proposed. Comparing two such separate boreo-nemoral alliances of the xerothermic vegetation with their central European counterparts reveals interesting relationships (Table 10). The *Tortello-Sedion* is positively characterised, whereas the Nordic alliance of the basiphilous semi-dry grasslands (*Filipendulo-Helictotrichion, Brachypodietalia pinnati* Korneck 1974, *Festuco-Brometea*) is a negatively characterised central syntaxon (Table 10). Nevertheless, *Tortello-Sedion* and *Filipendulo-Helictotrichion* have four shared differential taxa that separate them from the corresponding more southerly distributed alliance. Two of these (*Festuca ovina* s.str., *Thymus serpyllum*) are quite faithful to sandy dry grasslands of the subclass *Koelerio-Corynephoronea* and are almost absent from *Sedo-Scleranthenea* and *Festuco-Brometea* communities in central Europe (cf. BERG et al. 2001, 2004). Their sociological amplitude seems to be greatly expanded in the Nordic countries, a phenomenon which can be found in other xerothermic species as well (LÖBEL & DENGLER subm.). When we examine growth forms and ecological types in

Table 10: Relationships between the Nordic and central European syntaxa demonstrated on the basis of a comparison within the orders *Alyso-Sedetalia* (*Koelerio-Corynepherea*) and *Brachypodietalia pinnati* (*Festuco-Brometea*).

Tab. 10: Beziehungen zwischen den nordischen und mitteleuropäischen Syntaxa im Vergleich der Ordnungen *Alyso-Sedetalia* (*Koelerio-Corynepherea*) und *Brachypodietalia pinnati* (*Festuco-Brometea*).

	<b>Basiphilous dry grasslands of shallow, skeletal soils</b>	<b>Basiphilous semi-dry grasslands</b>
<b>Order</b>	<i>Alyso alyssoidis-Sedetalia</i>	<i>Brachypodietalia pinnati</i>
<b>Nordic alliance</b>	<i>Tortello tortuosae-Sedion albi</i>	<i>Filipendulo-Helictotrichion</i>
	– positively characterised –	– central syntaxon –
<b>Central European alliance(s)</b>	<i>Alyso alyssoidis-Sedion</i>	<i>Bromion erecti</i> and <i>Cirsio-Brachypodion pinnati</i>
	– central syntaxon –	– positively characterised –
<b>Differential taxa of the Nordic alliance</b>		
– joint	<i>Arabis hirsuta</i> , <i>Festuca ovina</i> s. str., <i>Fissidens dubius</i> , <i>Thymus serpyllum</i>	
– mesophytic and slightly acidophytic graminoids	<i>Bromus hordeaceus</i>	<i>Agrostis capillaris</i> , <i>Avenula pratensis</i> , <i>Danthonia decumbens</i> , <i>Festuca rubra</i> , <i>Luzula campestris</i>
– large, competitive mosses	<i>Homalothecium lutescens</i>	<i>Dicranum scoparium</i> , <i>Plagiomnium affine</i>
– acrocarpous mosses and lichens	numerous taxa	–
– indicators of temporary water logging	<i>Agrostis stolonifera</i> , <i>Linum catharticum</i> , <i>Sagina nodosa</i> ,...	–
<b>Species densities of the Nordic communities compared to the central European ones</b>	more than twice as high! (mostly caused by cryptogams)	similar to slightly higher

the xerothermic communities of northern Europe, mesophilous graminoids as well as large bryophytes (probably also fruticose lichens) are much more frequent than in the corresponding central European communities. The *Tortello-Sedion* differs from the *Filipendulo-Helictotrichion* and also the *Galio-Geranion* by additionally accommodating numerous small acrocarpous mosses and lichens as well as some taxa of temporarily moist soils.

### 6.5. Implications for nature conservation

The basiphilous dry grasslands of shallow, skeletal soils in northern Europe are of great importance for nature conservation because of their high contribution to biodiversity (extremely high species densities, markedly floristic and ecological differentiation between the syntaxa). Moreover, the suballiance *Helianthemo-Tortellenion* with its four associations is endemic to the four alvar regions (Öland, Gotland, Kinnekulle, western Estonia) with their small overall area. These communities also contain several endemic taxa. According to available information, the largest, most diverse and best-developed stands, i.e. those containing most of the diagnostic species, occur on the Great Alvar of southern Öland (cf. ROSÉN & VAN DER MAAREL 2000).

The unique value of alvar vegetation is well known and widely accepted. These vegetation types have accordingly been included in Annex I of the Habitats Directive of the European Union as priority habitat 6280 ('Nordic alvar and precambrian calcareous flatrocks'; cf. EUROPEAN COMMISSION 2003). Alvar vegetation essentially is semi-natural and thus the maintenance of the open landscape depends on grazing by cattle, sheep, and horses, although extreme droughts may slow down the tree and shrub encroachment process

(ROSÉN & VAN DER MAAREL 2000). Despite changing grazing intensities, the Great Alvar of southern Öland, comprising more than 200 km<sup>2</sup>, has been largely kept open for several thousand years (ROSÉN & VAN DER MAAREL 2000). Recently, a large-scale restoration project was set up in the Great Alvar with the aim to re-introduce grazing on abandoned areas and clear-cut the scrub encroachment (ROSÉN & VAN DER MAAREL 2000). However, the situation in the other alvar regions is worse. From the 1930s to the year 2000, on Saaremaa and the adjacent smaller island of Muhu, the total area of alvar grasslands (including moist types) decreased from 260 km<sup>2</sup> to 78 km<sup>2</sup>, mostly due to the cessation of the traditional use as pastureland (HELM et al. 2006). A part of the remaining alvar areas on Saaremaa is now included in the Vilsandi national park. The park management has decided to allow the entire reserve to revert to natural dynamics, this despite the fact that dry alvar grasslands are protected under European legislation and are also listed as nationally rare and threatened plant communities (PAAL 1998). In Estonia, rare plant species are concentrated in the western parts of the islands of Saaremaa and Hiiumaa and the majority depend on moderate human impact for the maintenance of their habitats (KULL et al. 2002). Park policies should thus be changed to prevent the remaining highly valuable sites from rapid overgrowth with *Juniperus communis* and *Pinus sylvestris*. *Sedo-Scleranthenea* communities of non-alvar sites have not been in the focus of nature conservation in northern Europe. Doubtless due to the lack of a formal classification and a supra-regional overview, the distinctness, high species richness and small overall distribution ranges of these vegetation types have so far not been realised. Our study may thus help to shift the focus of nature conservation a bit more onto Nordic *Sedo-Scleranthenea* communities. The formal classification proposed here should furthermore serve to facilitate more precise and unambiguous communication about the vegetation of this important northern European ecosystem.

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Table 3: Abridged synoptic table of the *Alysso-Sedetalia* syntaxa in northern Europe. The numbers in the columns indicate the percentage presence degree in the case of associations, and the presence reference value in the case of superior syntaxa. Only diagnostic taxa and companion taxa with a presence reference value of at least 10 % at alliance level are shown. Non-terricolous taxa are excluded since they have been recorded only in part. The diagnostic value of the taxa is indicated by shadings and frames. If a species is additionally considered as characteristic for a superior syntaxon, this is noted to the left of its name. Species richness values refer to plot sizes between 2 m<sup>2</sup> and 10 m<sup>2</sup> (mostly 4 m<sup>2</sup>).

Tab. 3: Gekürzte Stetigkeitstabelle der nordeuropäischen Syntaxa der Ordnung *Alysso-Sedetalia*. Die Zahlen in den Spalten stellen bei den Assoziationen prozentuale Stetigkeitswerte und bei den höheren Syntaxa "Stetigkeitsreferenzwerte" dar. Es sind nur diagnostische Sippen sowie Begleiter mit einem Stetigkeitsreferenzwert von mindestens 10 % auf Verbandsniveau wiedergegeben. Nicht epigäische Taxa sind nicht dargestellt, da sie in den Aufnahmen nur teilweise berücksichtigt wurden. Der Kennwert der Sippen ist durch graue Hinterlegung und Rahmen wiedergegeben. Wenn eine Art zusätzlich als Kennart eines übergeordneten Syntaxons angesehen wird, ist dies links vom Artnamen angegeben. Die Artenzahlen beziehen sich auf Aufnahmeflächen zwischen 2 m<sup>2</sup> und 10 m<sup>2</sup> (überwiegend 4 m<sup>2</sup>).

- = character species of an alliance, suballiance or association
- = Charakterart auf Verbands-, Unterverbands- oder Assoziationsniveau
- = character species of superior rank or a transgressive character species
- = Charakterart höherer Syntaxa oder transgressive Charakterart
- = differential species
- = Differenzialart
- = negatively differentiating species within a species block
- = negativ differenzierende Art innerhalb eines Artenblocks

Syntaxon	All.	Suball. a	Suball. b	Assoc. 1	Assoc. 2	Assoc. 3	Assoc. 4	Assoc. 5	Assoc. 6	
Number of relevés	320	86	234	43	43	110	25	59	40	
Mean number of plant taxa (total)	45	37	49	30	43	44	48	50	53	
Mean number of vascular plants	19	19	19	17	21	20	12	20	23	
Mean number of bryophytes	16	10	19	7	12	17	23	17	18	
Mean number of lichens	10	7	11	5	9	7	13	13	11	
<b>Cl. Koelerio-Corynephoretea</b>										
C Sedum acre	V	60	87	46	93	81	42	40	44	58
Tortula ruralis agg. (total, see also Assoc. 2.4)	B	50	64	43	63	65	10	88	27	45
Androsace septentrionalis	V	5	6	5	12	.	1	8	10	.
<b>Subcl. Sedo-Scleranthenea</b>										
C Sedum album	V	68	40	82	56	23	71	96	78	83
Peltigera rufescens	L	46	65	37	42	88	45	40	36	25
Erophila verna	V	37	25	44	30	19	27	72	37	38
Bryum caespitium (incl. cf.-data)	B	24	17	28	33	.	32	32	27	20
Peltigera didactyla	L	9	4	12	7	.	7	24	12	3
<b>Ord. Alysso alyssoides-Sedetalia</b>										
C Acinos arvensis	V	56	45	61	53	37	61	48	63	73
Arenaria serpyllifolia subsp. serpyllifol.	V	54	81	41	74	88	28	32	61	43
Cladonia symphyocarpa	L	53	34	63	30	37	45	92	63	50
Thlaspi perfoliatum	V	3	4	2	7	.	.	.	.	8
<b>All. Tortello tortuosae-Sedion albi</b>										
C Ord. Ditrichum flexicaule	B	79	67	85	67	67	81	88	80	90
Cladonia pocillum	L	42	46	40	19	72	30	24	54	53
Encalypta rhaetocarpa	B	15	13	17	2	23	18	28	10	10
<b>Suball. a - Tortello tortuosae-Sedion albi (central suballiance)</b>										
D Cl. Ceratodon purpureus	B	33	59	20	53	65	24	16	25	13
Ci. Cerastium semidecandrum	V	20	48	7	35	60	11	.	15	.
Achillea millefolium subsp. millefolium	V	22	42	13	23	60	35	.	15	.
Subcl. Potentilla argentea agg.	V	16	37	5	37	37	5	.	12	3
Encalypta streptocarpa	B	15	24	10	14	33	19	8	10	3
<b>Assoc. 1 - Cladonia symphyocarpae-Sedetum albi (central association)</b>										
D Artemisia campestris subsp. campestris	V	39	35	40	63	7	25	20	46	70
Poa compressa	V	24	34	20	56	12	34	4	27	13
Ord. Saxifraga tridactylites	V	35	27	39	40	14	17	80	24	35
Brachythecium albicans	B	11	26	4	37	14	4	4	8	.
Allium oleraceum	V	7	19	1	33	5	1	.	2	3
Dactylis glomerata subsp. glomerata	V	7	14	3	28	.	2	.	2	8
Hypericum perforatum	V	11	11	12	21	.	18	4	12	13
Silene nutans subsp. nutans	V	10	13	8	21	5	2	.	14	15
<b>Assoc. 2 - Ditricho flexicaulis-Sedetum acris</b>										
C All. Bacidia bagliettoana	L	21	37	13	14	60	21	.	14	15
All. Tortella fragilis	B	15	30	8	2	58	24	.	7	.
Catapyrenium cinereum	L	6	18	1	.	35	.	.	2	.
D Cl. Cladonia furcata agg. (total, see also suball. b)	L	57	48	62	11	87	28	52	76	90
Festuca rubra	V	19	48	5	18	77	16	.	5	.
Bryoerythrophyllum recurvirostrum	B	31	36	28	.	72	13	48	22	30
Ci. Cladonia rangiformis	L	49	42	52	19	65	31	28	66	83
Lotus corniculatus	V	14	28	8	7	49	19	.	8	3
Taraxacum obliquum agg.	V	8	24	.	.	47	.	.	.	.
Antennaria dioica	V	10	22	3	.	44	2	.	8	3
Erigeron acer	V	8	23	0	2	44	1	.	.	.
Pimpinella saxifraga	V	12	26	5	7	44	8	.	10	3
Armeria maritima	V	8	23	.	5	40	.	.	.	.
Agrostis vinealis	V	8	18	3	.	35	4	.	5	3
Caloplaca cerina	L	5	15	.	.	30	.	.	.	.
Carex caryophylla	V	6	15	1	.	30	1	.	.	5
Euphrasia nemorosa	V	5	14	.	.	28	.	.	.	.
Leptogium gelatinosum	L	12	17	10	5	28	12	24	5	.
Homalothecium sericeum	B	10	19	5	12	26	1	4	7	10
Racomitrium canescens	B	10	16	7	5	26	3	8	5	10
Botrychium lunaria	V	4	12	.	.	23	.	.	.	.
Luzula campestris	V	4	13	.	2	23	.	.	.	.
Viola tricolor subsp. tricolor	V	4	12	1	.	23	.	.	2	.
Hypogymnia physodes	L	12	13	11	5	21	1	.	19	25
Solidago virgaurea	V	5	12	2	2	21	4	.	2	3
<b>Suball. b - Tortello rigentis-Helianthemion oelandici</b>										
C Cladonia subrangiformis	L	39	1	59	2	.	26	48	75	85
Encalypta vulgaris	B	31	.	46	.	.	25	64	36	60
Allium schoenoprasum var. alvarense (incl. cf.-data)	V	28	.	42	.	.	55	68	22	23
Ord. Hornungia petraea	V	29	7	39	14	.	5	56	46	50
Helianthemum oelandicum subsp. oelandicum	V	26	.	38	.	.	5	12	53	83
Trichostomum crispulum	B	25	.	37	.	.	26	44	37	40
All. Distichium capillaceum	B	27	9	36	2	16	25	52	36	30
Tortella rigens	B	22	.	33	.	.	31	48	24	30
Didymodon ferrugineus	B	19	1	28	2	.	24	56	19	13
Bryum elegans	B	17	1	26	2	.	31	36	15	20
Crepis tectorum subsp. pumila (incl. cf.-data)	V	16	.	24	.	.	50	28	19	.
Athalamia hyalina	B	13	1	18	2	.	17	16	20	20
Festuca oelandica (incl. cf.-data)	V	10	1	15	2	.	27	24	7	3
Gymnostomum aeruginosum	B	9	.	14	.	.	15	20	7	13
Leptogium schraderi	L	9	.	13	.	.	7	24	14	8
Silene uniflora subsp. petraea	V	3	.	4	.	.	8	3	5	5
Hieracium x dichotomum	V	2	.	2	.	.	4	.	2	3
D Cl. Thymus serpyllum subsp. serpyllum	V	45	4	65	7	.	40	52	81	88
Ord. Tortella inclinata	B	47	13	64	26	.	47	88	61	60
Fissidens dubius	B	39	11	53	5	16	75	4	61	70
Weissia brachycarpa (incl. cf.-data)	B	35	1	52	2	.	54	52	37	63
Agrostis stolonifera	V	35	5	51	7	2	95	44	51	13
Didymodon fallax	B	35	6	50	2	9	35	76	44	45
Scorpidium turgescens	B	25	1	37	2	.	41	56	31	18
Ord. Cerastium pumilum	V	25	4	36	7	.	23	56	36	30
Pleuridium acuminatum (incl. cf.-data)	B	23	.	34	.	.	23	60	29	25
Ord. Psora decipiens	L	23	1	34	2	.	19	56	37	23
Campyllum chrysophyllum	B	23	3	33	.	5	45	20	34	33
Subcl. Potentilla tabernaemontani	V	23	5	33	9	.	22	12	37	60
Thamnolia vermicularis var. subuliformis	L	19	.	29	.	.	20	36	58	.
Filipendula vulgaris	V	19	2	28	2	2	25	4	31	50
Myurella julacea	B	18	1	26	.	2	35	32	17	20
Ctenidium molluscum	B	15	3	22	.	5	30	24	22	10
<b>Assoc. 3 - Crepidio pumilae-Allietum alvarense</b>										
C Suball. Artemisia rupestris	V	9	.	14	.	.	44	.	2	8
D Sagina nodosa	V	23	28	20	19	37	58	20	3	.
Prunella vulgaris	V	14	10	16	12	7	48	4	10	3
Veronica spicata subsp. spicata	V	12	4	17	7	.	40	.	14	13
Leontodon autumnalis	V	16	19	15	9	28	36	12	7	5
Barbula unguiculata	B	10	8	11	7	9	25	4	8	5
Calliergonella cuspidata	B	5	.	7	.	.	25	.	3	.
Drepanocladus cossonii	B	6	.	8	.	.	25	.	5	3
<b>D Assoc. 3, 5 and 6 (against 4)</b>										
Anthyllis vulneraria	V	52	63	46	40	86	47	4	47	88
Galium verum subsp. verum	V	53	66	46	44	88	47	12	56	70
Linum catharticum	V	33	21	39	7	35	64	12	46	35
Plantago lanceolata	V	32	53	21	42	63	36	.	29	20
<b>Assoc. 4 - Fulgensio bracteatae-Poetum alpinae</b>										
C Suball. Fulgensia bracteata subsp. bracteata	L	28	.	41	.	.	29	84	32	20
Ord. Toninia sedifolia	L	25	7	34	2	12	21	76	29	8
Ci. Tortula calcicolens	B	20	3	29	5	.	5	76	14	20
Suball. Didymodon rigidulus	B	19	.	28	.	.	17	68	14	13
Suball. Mycobolium lurida	L	18	.	28	.	.	13	68	19	10
Suball. Schistidium atrofusum	B	13	.	20	.	.	11	56	3	10
Fulgensia fulgens	L	9	.	14	.	.	4	40	7	3
Suball. Tortella densa	B	11	.	16	.	.	8	40	10	5
Suball. Ceratodon conicus	B	7	1	10	2	.	4	28	5	3
Squamarina cartilaginea	L	3	.	5	.	.	1	16	2	.
Squamarina lentigera	L	2	.	4	.	.	1	12	2	.
D Poa alpina	V	22	18	24	35	.	9	76	7	3
Ci. Tortula ruraliformis	B	22	8	29	16	.	6	64	12	35
Bromus hordeaceus subsp. hordeaceus	V	35	44	31	47	40	21	60	36	5
Collema cristatum	L	12	.	18	.	.	5	60	.	8
Leptogium lichenooides	L	24	25	24	.	49	10	60	17	8
Collema crispum	L	14	1	21	2	.	12	52	12	8
Bryum argenteum	B	25	28	23	28	28	14	48		

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Table 6: Relevés of the *Fulgensio bracteatae-Poetum alpinae* from northern Europe. For the abbreviations, see text.

Tab. 6: Aufnahmen des *Fulgensio bracteatae-Poetum alpinae* aus dem nördlichen Europa. Die verwendeten Abkürzungen sind im Text erklärt.

Serial number	Assoc.	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25
Relevé number	n =	A02	A65	A72	A82	A85	A89	A105	A122	A125	A126	A128	A130	A136	A137	A145	A152	AB13	AB16	AB22	AB26	E81	E84	E88	T18	T19
Origin		sO	sO	sO	sO	sO	sO	sO	sO	sO	sO	sO	sO	sO	sO	sO	sO	sO	sO	sO						
Aspect		-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Inclination [%]		0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Cover herb layer [%]		18	20	10	15	50	25	8	10	25	5	4	8	15	10	20	10	35	10	15	10	10	40	50	20	12
Cover cryptogam layer [%]		35	40	40	40	70	60	40	28	20	35	30	10	20	60	35	35	25	15	50	10	8	60	45	50	25
Plot size [m <sup>2</sup> ]		4	4	4	4	4	4	4	4	4	4	4	4	4	4	4	4	4	4	4	4	4	4	4	4	4
Species richness (total)		48	75	34	54	44	72	34	50	44	49	40	49	38	36	54	36	47	61	51	60	48	57	54	57	22
Species richness (vascular plants)		12	17	11	9	9	28	4	10	10	4	6	20	5	4	19	14	12	18	13	17	11	9	12	12	7
Species richness (bryophytes)		23	40	17	21	24	31	21	24	20	27	24	16	17	20	18	12	20	24	26	25	19	33	33	30	10
Species richness (lichens)		13	18	5	23	11	13	8	16	13	17	10	13	16	12	16	9	14	18	11	18	17	15	9	14	4
Species richness (only terricolous taxa)		47	73	34	50	44	71	30	50	44	46	39	45	38	36	54	36	47	60	51	55	48	56	54	52	22
Number of undetermined terricolous crustose lichens		1	0	1	2	2	0	0	1	3	1	0	1	0	1	1	1	1	5	2	3	4	2	2	0	0

**Assoc. 4 - Fulgensio bracteatae-Poetum alpinae**

<b>C</b>	<i>Fulgensia bracteata</i>	L	84	2m	2m	2m	2m	1	2m	1	1	2m														
	<i>Toninia sedifolia</i>	L	76	2m	2m	2m	2m	2m	2m	1	2m															
	<i>Tortula calcicolens</i>	B	76	2m	2m	1	2m	2m	2m	2m	2m	1	2m	1	2m	2m	1	1	1	1	1	2m	2m	2m	2m	2m
	<i>Didymodon rigidulus</i>	B	68	2m																						
	<i>Mycobilimbia lurida</i>	L	68	2m																						
	<i>Schistidium atrofuscum</i>	B	56	2a	2m	2a	2m	2m	2m	2m	2m	2m														
	<i>Fulgensia fulgens</i>	L	40	2m																						
	<i>Tortella densa</i>	L	40	2m																						
	<i>Ceratodon conicus</i>	B	28	2m																						
	<i>Squamarina cartilaginea</i>	L	16	2m																						
	<i>Squamarina lentigera</i>	L	12	2m																						
<b>D</b>	<i>Poa alpina</i>	V	76	1	+	2m	1	+	2m	1	+	2m	1	+	2a	1	1	2m	2m	2m	2a	+	1	1	1	+
	<i>Collema cristatum</i>	L	60	2m																						
	<i>Leptogium lichenoides</i>	L	60	2m																						
	<i>Collema crispum</i>	L	52	2m																						
	<i>Bryum argenteum</i>	B	48	2m																						
	<i>Leptogium gelatinosum</i>	L	24	2m																						
<b>D with Crepidio-Allietum</b>	<i>Festuca oelandica</i>	V	24	1	+	2m																				
<b>D with Gypsophilo-Globularietum</b>	<i>Tortula ruraliformis</i>	B	64	2m	2a	2a	1	1	1																	
<b>D with Crepidio-Allietum and Helianthemo-Galietum</b>	<i>Bromus hordeaceus</i> subsp. <i>hordeaceus</i>	V	60	1	+	2m																				
	<i>Agrostis stolonifera</i>	V	44	1	+	2m																				
<b>D with Helianthemo-Galietum and Gypsophilo-Globularietum</b>	<i>Hornungia petraea</i>	V	56	1	+	2m																				
	<i>Thamnia vermicularis</i> var. <i>subuliformis</i>	L	20	2m																						

**Suball. Tortello rigidus-Helianthemion oelandici**

<b>C</b>	<i>Allium schoenoprasum</i> var. <i>alvarense</i>	V	68	+	+	1	1	2m																		
	<i>Encalypta vulgaris</i>	B	64	2m	1	2m	1	1	2m																	
	<i>Didymodon ferrugineus</i>	B	56	2m																						
	<i>Distichium capillaceum</i>	B	52	2m																						
	<i>Cladonia subrangiformis</i>	L	48	2m																						
	<i>Tortella rigens</i>	B	48	2m																						
	<i>Trichostomum crispulum</i>	B	44	2m																						
	<i>Bryum elegans</i>	B	36	2m																						
	<i>Crepis tectorum</i> subsp. <i>pumila</i>	V	28	2m																						
	<i>Leptogium schraderi</i>	L	24	2m																						
	<i>Gymnostomum aeruginosum</i>	B	20	2m																						
	<i>Athalamia hyalina</i>	B	16	1	+	2m																				
	<i>Helianthemum oelandicum</i> subsp. <i>oelandicum</i>	V	12	2m																						
	<i>Silene uniflora</i> subsp. <i>petraea</i>	V	8	2m																						
	<i>Sisymbrium spinum</i>	V	4	2m																						
<b>D</b>	<i>Tortella inclinata</i>	B	88	2m																						
	<i>Didymodon fallax</i>	B	76	2m																						







