

Nutrient-poor grasslands on siliceous soil in the lower Aar valley (Middle Hesse, Germany) – neglected vegetation types in the intersection range of four classes

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Abstract

In the lower siliceous uplands of Central Europe, various types of nutrient-poor grasslands are widespread and grow intermingled. These species-rich grasslands, often dominated by taxa of the *Festuca ovina* aggregate, comprise various phytosociological classes. They are remnants of a historic rural landscape and are of conservation importance. Few studies on such grasslands are available and there has been disagreement in assigning them to appropriate habitat types or syntaxa.

We investigated such nutrient-poor grasslands in the lower Aar valley (Middle Hesse, Rhenish Massif). We surveyed 104 vegetation plots distributed throughout the valley and identified syntaxa to (sub)association level. We carried out supervised classification combining cluster analysis, *a priori* assignment to classes based on prevailing diagnostic species, and regional refinement based on phi-value maximisation of the units. As a result, we classified five associations within four classes: *Polytricho piliferi-Festucetum tenuifoliae*/*Galio hircynici-Deschampsietum flexuosae* and *Festuco rubrae-Genistelletum sagittalis* (*Calluno-Ulicetea*), *Jasione montanae-Festucetum ovinae* (*Koelerio-Corynephoretea*), *Gentiano-Koelerietum pyramidatae* (*Festuco-Brometea*) and *Arrhenatheretum elatioris* (*Molinio-Arrhenatheretea*). Ecologically, soil acidity (resulting from Ca concentrations of the bedrock) was the main cause of floristic dissimilarity of the grasslands and thus community differentiation. Many stands grew on soils with intermediate pH and showed a peculiar mixture of basiphilous and acidophilous species. We conclude that (i) our approach of supervised classification yields convincing reproducible results when a syntaxonomic system is adapted top-down to a geographically restricted area, (ii) nutrient-poor siliceous grasslands dominated by taxa of the *Festuca ovina* aggregate can be well assigned to ecologically meaningful syntaxa, and (iii) the nutrient-poor siliceous grasslands of the Lahn-Dill Highlands are of high conservation relevance and in urgent need of protection.

Zusammenfassung: Silikatmagerrasen im unteren Aartal (Lahn-Dill-Bergland, Mittelhessen) – bislang wenig beachtete Vegetationstypen im Schnittbereich von vier Klassen

In den Silikat-Mittelgebirgen Mitteleuropas sind verschiedene Typen von Magerrasen weit verbreitet und oft eng miteinander verzahnt. Diese oftmals von Schafschwingel-Arten aus dem *Festuca ovina*-Aggregat dominierten, artenreichen Bestände stehen im Grenzbereich mehrerer pflanzensoziologischer Klassen. Als Reste einer historischen Kulturlandschaft besitzen sie eine hohe Naturschutzbedeutung. Bislang wurden über diese Magerrasen nur wenige Studien publiziert. Bei einigen Pflanzengesellschaften war unklar, zu welchen Habitattypen und Syntaxa sie zählen.

Wir untersuchten die Silikat-Magerrasen des unteren Aartals (Mittelhessen, Rheinisches Schiefergebirge). Verteilt über das Tal wurden 104 Vegetationsaufnahmen erstellt und bis hin zur Ebene der Assoziation bzw. Subassoziation klassifiziert. Dazu führten wir eine Clusteranalyse und (auf Grundlage eines übergeordneten Systems) eine *a priori*-Zuordnung der Aufnahmen zu Klassen durch. Anschließend wurde die Güte der Gliederung durch phi-Wert-Maximierung weiter erhöht. Im Ergebnis unterschieden wir fünf Assoziationen, die zu vier Klassen gehören: *Polytricho piliferi-Festucetum tenuifoliae*/*Galio hircynici-Deschampsietum flexuosae* und *Festuco rubrae-Genistelletum sagittalis* (*Calluno-Ulicetea*), *Jasione montanae-Festucetum ovinae* (*Koelerio-Corynephoretea*), *Gentiano-Koelerietum pyramidatae* (*Festuco-Brometea*) und *Arrhenatheretum elatioris* (*Molinio-Arrhenatheretea*). Boden- und Zeigerwertanalysen zeigten, dass die (vor allem durch unterschiedliche Ca-Gehalte bestimmte) Bodenazidität den Hauptfaktor für die floristische Unterschiedlichkeit und damit die Differenzierung der Gesellschaften bildet. Viele Bestände wuchsen auf Böden mit mittlerer Reaktion und wiesen eine ungewöhnliche, jedoch für das Gebiet charakteristische Mischung aus basi- und azidophilen Arten auf. Wir schlussfolgern, dass (i) unsere *top-down*-Anwendung eines übergeordneten syntaxonomischen Systems

auf ein geographisch begrenztes Gebiet zu einem befriedigenden und reproduzierbaren syntaxonomischen Ergebnis führt, (ii) die von Taxa aus dem *Festuca ovina*-Aggregat aufgebauten Silikat-Magerrasen des unteren Aartals gut in ökologisch sinnvolle Syntaxa klassifiziert werden können, und (iii) die Silikat-Magerrasen des Lahn-Dill-Berglands eine hohe naturschutzfachliche Bedeutung besitzen und daher effektiv geschützt werden sollten.

Keywords: *Calluno-Ulicetea*, classification, *Festuco-Brometea*, grassland conservation, *Koelerio-Corynephoretea*, Lahn-Dill Highlands, *Molinio-Arrhenatheretea*, ordination, phi value, Rhenish Massif, soil analysis, syntaxonomy

1. Introduction

Acidophilous grasslands of the *Koelerio-Corynephoretea* and *Calluno-Ulicetea*, and basiphilous grasslands of the *Festuco-Brometea* rarely co-occur, as generally the bedrock of a region results in either acidic or basic soil. The nutrient-poor pastures of the Lahn-Dill Highlands (Hesse, central Germany) dominated by taxa of the *Festuca ovina* aggregate are thus a peculiarity, as here grasslands which developed on soils of different (and intermediate) acidity grow side by side. They originated and were maintained in this marginal region through centuries of low-intensity farming on common land (*Allmende*) as well as on private land. Nowadays, they are remnants of a highly varied historic rural landscape and have become rare in other parts of Germany and Western Europe. Few studies exist on the nutrient-poor grasslands on siliceous soil in the Lahn-Dill Highlands (e.g. BERGMEIER 1987, OTTE et al. 2008) and adjacent regions (HÜLBUSCH 1982, GREGOR 2001, SCHMITT & FARTMANN 2006). However, other studies have covered the mesic to wet grasslands (*Molinio-Arrhenatheretea*; NOWAK 1990, 1992), local vegetation surveys, land use histories and conservation issues (NOWAK 1988, 1991a, 1991b) as well as recent land use changes affecting the diversity of the grasslands and landscape structure in this region (WALDHARDT & OTTE 2003, HIETEL et al. 2004, WELLSTEIN et al. 2007, OTTE et al. 2008).

Nutrient-poor grasslands on siliceous soil dominated by various taxa of the *Festuca ovina* aggregate are widespread in the uplands of Central Europe but their syntaxonomic treatment has been particularly inconsistent (reviewed in GREGOR 2001), i.e. similar communities had been placed in different alliances, orders, and classes because they often show combinations of species considered as diagnostic for different syntaxa (HÜLBUSCH 1982, BERGMEIER 1987, GREGOR 2001, SCHMITT & FARTMANN 2006). Here we aim to disentangle this peculiar floristic mixture by formalised “top-down” assignment on the basis of class character species and validated the result with a numerical “bottom-up” method to create a comprehensible classification. Moreover, we analysed soil conditions to ensure an ecologically meaningful classification.

This paper is the first study addressing the plant communities and specific conservation relevance of the dry to mesic siliceous grasslands in the Lower Aar valley of the Lahn-Dill Highlands. Although the geographical scope and limitations of the data set make this a local case study, inductive generalization is possible in terms of (i) **the methodical approach**, combining numerical classification and ordination of a local data set with findings derived from a much larger body of data; (ii) **syntaxonomy**, linking the classified plant communities with the widely accepted (and at the same time controversial) syntaxonomic scheme; (iii) **soil analysis**, understanding the factors underlying community differentiation, and (iv) **national and international conservation schemes**, asking whether the previously neglected siliceous nutrient-poor grasslands of the Lahn-Dill Highlands are covered by habitat types listed in Annex I of the EU Habitats Directive.

2. Study area

The study area is located in the district Lahn-Dill-Kreis in west-central Hesse (Germany) and comprises the lower Aar valley between the Aar reservoir and the Aar river mouth near Herborn (N 50°40'10"–50°43'20", E 8°19'00"–8°28'10"; Fig. 1). It belongs to the Lahn-Dill Highlands (*Lahn-Dill-Bergland* = *Gladenbacher Bergland*), which are part of

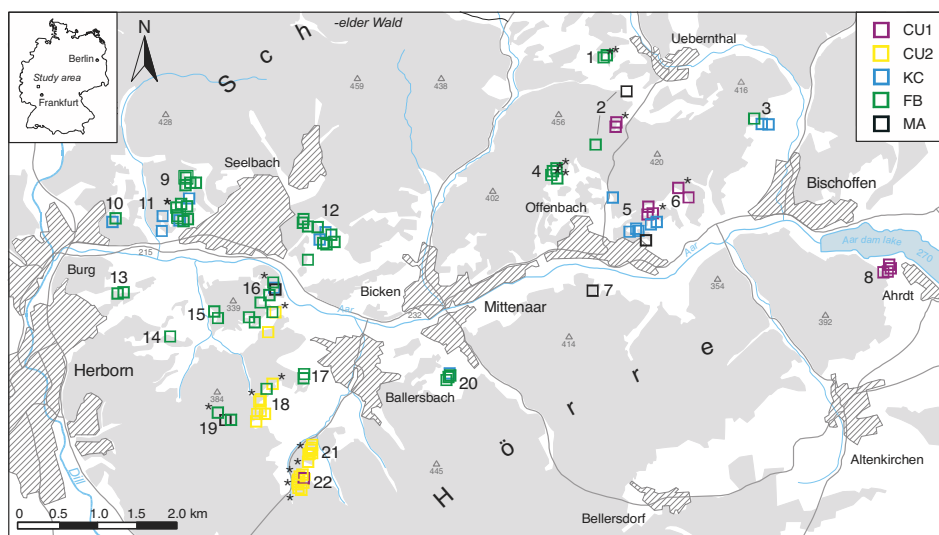


Fig. 1: The study area and the location of the 22 study sites. The site numbers correspond to Table 1. The coloured quadrats indicate the location of 104 vegetation plots. CU1 = *Polytricho-Festucetum tenuifoliae/Galio-Deschampsietum flexuosae*, CU2 = *Festuco-Genistetum*, KC = *Jasiono-Festucetum ovinae*, FB = *Gentiano-Koelerietum*, MA = *Arrhenatheretum*. Forest areas are indicated in grey. Plots where soil samples were taken are indicated by asterisks ("*").

Abb. 1: Das Untersuchungsgebiet und die Lage der 22 Untersuchungsflächen. Die Nummern der Flächen entsprechen Tabelle 1. Die farbigen Quadrate zeigen die Lage der 104 Aufnahmeflächen an. Die Bedeutung der Assoziationskürzel kann der englischen Legende entnommen werden. Waldgebiete sind grau hinterlegt. Aufnahmeflächen, in denen Bodenanalysen durchgeführt wurden sind mit Sternchen ("*") gekennzeichnet.

the Rhenish Massif (*Rheinisches Schiefergebirge*), and comprises three natural regions: *Schelder Wald* (in the north west), *Zollbuche* (in the north east) and *Hörre* (in the south) (KLAUSING 1988). The studied area is strongly dissected by valleys, and a large proportion of the area is covered by forests (mainly at higher elevations). The 22 study sites were located around the villages Herborn-Burg (abbreviated with Bu in the vegetation table), Herborn-Seelbach (Se), Mittenaar-Ballersbach (Ba), Mittenaar-Bicken (Bi), Mittenaar-Offenbach (Of), Siegbach-Uebernthal (Ue), Bischoffen (Bi) and Ahrdt (Ah), between 235 and 385 m a.s.l. and mostly at mid-slope (Table 1, Fig. 1). Study sites located south of the Aar river belong to the Natura 2000 site "Grünlandkomplex von Herborn-Seelbach bis Ballersbach und Aar-Aue" (EU 5316-302), while the easternmost study site is part of the nature reserve "Wacholderheide bei Ahrdt".

The bedrock of the sites includes Devonian and Carboniferous argillaceous shales (*Tonschiefer*; abbreviated with TS in the vegetation tables), diabase (Di), greywacke from the upper Devonian period (GW), fine-grained sand- or siltstone from the lower Devonian period (SS) and *Schalstein* with pockets of corallian limestone (Sch) (KÖNIGLICH PREUSSISCHE GEOLOGISCHE LANDESANSTALT 1907, HESSISCHES LANDESAMT FÜR BODENFORSCHUNG 1970). Soil-forming substrates occur often as a mixture due to solifluction during the ice age, and sometimes soil contains loess loam. The soils are for the most part shallow and stony, mostly lime-deficient but moderately basic due to high amounts of magnesium. Soils on *Schalstein* are rich in lime and those over greywacke and sandstone are nearly lime-free and therefore acid. Soil types are brown earths and rankers (or intermediate types) (on argillaceous shale, sandstone and greywacke) as well as brown earth-rendzinas (on diabase and *Schalstein*). The climate of the study area is moderately summer-warm and moderately humid. Mean annual temperature is around 8.5 °C, while mean annual precipitation ranges from 700 to 750 mm (DEUTSCHER WETTERDIENST 1981). The macroclimate is sub-Atlantic.



Fig. 2: Typical landscape of the lower Aar valley. Higher elevations are covered by forests and slopes by nutrient-poor grasslands, which often develop into large *Cytisus scoparius* coppices after abandonment. (Photo: V. Schmucker, 2010)

Abb. 2: Typische Landschaft im unteren Aartal. Die Hochlagen werden von Wäldern eingenommen und die Hänge von Magerrasen und -wiesen, die sich ausbleibender Nutzung (wie hier) oft zu Besen-
ginstergebüsch (Cytisus scoparius) entwickeln. (Foto: V. Schmucker, 2010)

The nutrient-poor grasslands of the Aar valley developed over centuries of low-intensity land-use. Many stands are relicts of former common land (*Allmende*) which date back to the Middle Ages. The *Hutungen*, pastures on common land, were usually grazed by the whole cattle stock of a village or (less commonly) by sheep flocks led by a municipal shepherd. Between April and the beginning of winter, cattle grazed daily on the pastures, so that the swards remained low with open patches. Further pasture management included manual removal of weeds and shrubs. The pastures remained unfertilized and further nutrient-loss may have occurred due to erosion of the top soil.

In the Aar valley, *Allmende* land-use persisted until the first half of the 20th century, and was practised in some parts of the Lahn-Dill Highlands until the 1960s. After that, most common pastures were either afforested with conifers or abandoned, leading to shrub encroachment. In the 1960s, large-scale abandonment in the area became known as *Sozialbrache*, a term soon adopted widely even outside the area to describe similar farmland abandonment due to changes in the socio-economic conditions (NOWAK 1992, also see SCHULZE VON HANXLEDEN 1972). Some former common pastures were transformed into fenced pastures, but most of the grasslands investigated in this study are currently grazed by mobile sheep flocks, some after a fallow period.

Nutrient-poor grasslands on private land, in contrast, occur mainly on former hay meadows and arable fields. They are usually much younger than the medieval common pastures. Until the 1970s, farm holdings in the Aar valley were rarely larger than 5 ha (HESSISCHER MINISTER FÜR LANDWIRTSCHAFT UND FORSTEN 1969), and thus private land was primarily used for arable farming or hay production (see NOWAK 1988, 1992 for further details). Drastic socio-economic changes after World War II meant, however, that arable farming in the Aar valley ceased almost completely (HIETEL et al. 2004), and low yielding

Table 1: Overview of the 22 study sites and their plant communities. ¹⁾ For parishes, see Section 2. ²⁾ Mean value of relevés. Substrates: Di = diabase, GW = greywacke, Sch = Schiefer, SS = sandstone or Siltstein, TS = Argillaceous shales (*Tonschiefer*). Associations: CU1 = *Polytricho-Festucetum tenuifoliae/Galio-Deschampsietum flexuosae*, CU2 = *Festuco-Genistetum*, KC = *Jasiono-Festucetum ovinae*, FB = *Gentiano-Koelerietum*, MA = *Arrhenatheretum*.

Tabelle 1: Übersicht der 22 Untersuchungsflächen und ihrer Pflanzengesellschaften. ¹⁾ Die Gemarkungen siehe in Kapitel 2. ²⁾ Mittel der Aufnahmen. Die Bedeutung der Substrat- und Assoziationskürzel kann der englischen Legende entnommen werden.

No.	Study site	Parish ¹⁾	German grid coordinates ²⁾	Elevation (m a.s.l.) ²⁾	Slope (°) ²⁾	Substrate (# relevés)	Association (# relevés)
1	Zaubach	Ue	345863/562098	370	12	Di (2)	FB (2)
2	Königsköppel	Of, Ue	345874/562010	371	9	Di (1), SS (1), TS (2)	CU1 (2), FB (1), MA (1)
3	Sandberg	Bis	346075/562008	318	22	GW (3)	KC (2), FB (1)
4	Blätterwand	Of	345794/561939	356	9	Di (1), Sch (3)	FB (4)
5	Wörbelberg	Of	345913/561874	334	10	GW (10)	CU1 (3), KC (6), MA (1)
6	Wildestein	Of	345967/561914	340	4	GW (2)	CU1 (2)
7	Offenbach-Süd	Of	345846/561780	300	16	GW (1)	MA (1)
8	NSG Wacholderheide bei Ahrdt	Ah	346246/561809	280	1	SS (4)	CU1 (4)
9	Bornberg	Se	345301/561920	324	15	Di (3)	KC (1), FB (3)
10	Elkersberg	Bu	345197/561876	303	9	Di (2)	KC (1), FB (1)
11	Forstkopf	Se	345284/561882	282	18	Di (9)	KC (3), FB (6)
12	Horchberg	Se	345474/561855	310	9	Di (11)	KC (2), FB (9)
13	Eichenberg	Se	345206/561777	250	17	TS (2)	FB (2)
14	Schmidlberg	Se	345273/561718	305	2	Di (1)	FB (1)
15	Hain-West	Se	345336/561748	250	17	Di (2)	FB (2)
16	Hain-Ost	Se, (Ba)	345405/561760	267	15	Di (7), SS (1), TS (2)	CU2 (2), KC (1), FB (6), MA (1)
17	Ballersbach-West	Ba	345455/561665	298	22	Di (2)	FB (2)
18	Niederbachsberg	Ba, (Se, Of)	345398/561626	348	7	Di (1), TS (7)	CU2 (7), FB (1)
19	Sohl	Ba	345347/561608	358	5	Di (2), TS (1)	FB (2), MA (1)
20	Hemberg	Bi	345651/561664	294	19	GW (4)	KC (1), FB (3)
21	Sportplatz Ballersbach-Nord	Ba	345464/561561	304	4	TS (7)	CU2 (7)
22	Sportplatz Ballersbach-Süd	Ba	345450/561520	332	13	Di (4), TS (5)	CU2 (9)

arable land on shallow, dry and stony soil (*Scherbenäcker*) was left to transform into pastures or meadows through natural succession. In contrast to these younger grasslands, the historic meadows and common pastures on shallow soil have a long continuity as a nutrient-poor habitat, as any available fertiliser was preferentially applied to crop-fields.

Today, nutrient-poor grasslands in the Aar valley are primarily managed to avoid scrub encroachment and their commercial value is minimal. In recent decades, most of the nutrient-poor meadows on the slopes of the study area have been grazed by sheep, while the more productive meadows in the valleys are used for hay making.

3. Methods

3.1 Vegetation sampling

Vegetation was sampled from mid-May to mid-August 1994, attempting to include all recognisable types of nutrient-poor grasslands (SCHMIEGE 1995). Grassland fallows were also sampled if there was little visible effect of succession on the vegetation. In total, 104 vegetation plots were sampled; plot coordinates are available in Appendix 1. With the exception of 12 slightly smaller (10–18 m²) or larger (24–25 m²) plots, all other relevés were carried out on 20 m². All terricolous vascular plants, bryophytes and lichens were recorded, and their cover-abundance value estimated according to the modified Braun-Blanquet scale of REICHELT & WILMANN (1973). Bryophytes, lichens and the taxa of *Festuca ovina* aggregate were determined in the lab with the help of a microscope. Vascular plant nomenclature follows BUTTLER et al. (2011) for species and subspecies and WISSKIRCHEN & HAEUPLER (1998) for aggregates, while bryophytes are named according to KOPERSKI et al. (2000) and lichens according to SCHOLZ (2000).

3.2 General environmental and vegetation parameters

Slope and aspect were estimated in the field with the help of an inclinometer and a compass. From this, we calculated the heat load index (OLSSON et al. 2009). Information on geology was derived from geological maps, scale 1:25,000 (KÖNIGLICH PREUSSISCHE GEOLOGISCHE LANDESANSTALT 1907, HESSISCHES LANDESAMT FÜR BODENFORSCHUNG 1970). Land use was estimated by observation and asking land owners and users. The following land-use types were distinguished: C = common pasture (*Triftweide*), P = fenced pasture (*Standweide*), M = hay meadow, F = fallow.

We calculated mean un-weighted Ellenberg indicator values (EIVs) for temperature, nutrients, moisture and soil reaction (ELLENBERG et al. 2001), and cover-weighted mean indicator values of grassland usage (UIVs; i.e. trampling tolerance, cutting tolerance, grazing tolerance, fodder quality) according to BRIEMLE et al. (2002). Finally, we assessed the number of endangered plants per plot, based on the red lists of Germany (KORNECK et al. 1996) and Hesse (BOTANISCHE VEREINIGUNG FÜR NATURSCHUTZ IN HESSEN 2011).

3.3 Soil sampling and analyses

Soil analyses were carried out for 21 vegetation plots (SCHMIEGE 1995) (marked with * in the vegetation table), belonging to three out of the five associations distinguished later. The soil type was determined according to BUNDESANSTALT FÜR GEOWISSENSCHAFTEN UND ROHSTOFFE & GEOLOGISCHE LANDESÄMTER IN DER BUNDESREPUBLIK DEUTSCHLAND (1982) using a soil core drawn with a geological drill (*Pürckbauer*). In November 1994, five soil cores up to 30 cm depth were taken at random locations within the same plots with a core cutter of 5 cm diameter. The cores were split into the Ah horizon and the B horizon (sometimes including transitions to the Cv horizon) and joined into mixed samples per plot and horizon for the further analyses. Soil pH was determined electrometrically in demineralised water and a suspension of one part fresh soil in 2.5 parts saturated KCl solution after shaking for a short period. The available field capacity in the effective soil horizon, i.e. soil water content between pF 1.8 and 4.2, was estimated according to BUNDESANSTALT FÜR GEOWISSENSCHAFTEN UND ROHSTOFFE & GEOLOGISCHE LANDESÄMTER IN DER BUNDESREPUBLIK DEUTSCHLAND (1982). For all subsequent analyses, the samples were dried at 105 °C, ground and sieved with 2 mm mesh width. For titrimetric determination of the potential cation exchange capacity (CEC_{pot}), the fine earth samples were mixed with BaCl₂ solution at pH 8.1, and the exchange then was carried out with CaCl₂ solution of the same alkalinity. The actually exchanged basic (Ca²⁺, K⁺, Mg²⁺, Na⁺) and acidic ions (Al³⁺, Fe²⁺, H⁺, Mn²⁺) were measured with atomic adsorption spectroscopy (AAS). The base saturation was calculated as a

fraction of basic ions among all exchanged ions. Finally, the C and N content in the fine earth was measured with a C/N analyser (CHN-Rapid-Analysator, Heraeus), and C/N ratio as well as organic matter content calculated from these figures.

3.4 Vegetation classification

To classify the grasslands of the Aar valley, we used a four-step approach. First, we applied a widely used numerical classification method in PC-ORD 5.0 (MCCUNE & GRACE 2002). For this, the cover-abundance values of the species were first back-transformed to the mean cover (in %) of the respective class, then subjected to a $\log(x + 1)$ transformation in order to avoid the domination of a few highly abundant species in the cluster process. Then we applied flexible beta clustering with $\beta = -0.25$ and Bray-Curtis as distance measure. We tried different cluster resolutions, but found the four-cluster solution to be best interpretable in ecological terms, which thus was used for the next steps.

Second, we assigned relevés to classes in a top-down approach as applied by DENGLER et al. (2006), MICHL et al. (2010) and WILLNER (2011). According to structure and overall floristic composition, four vegetation classes had to be taken into consideration: *Calluno-Ulicetea*, *Koelerio-Corynepherea*, *Festuco-Brometea* and *Molinio-Arrhenatheretea*. We largely relied on the quantitative assessments compiled in BERG et al. (2001, 2004) for Mecklenburg-Vorpommern, as this work represents the only syntaxonomic treatment within Germany that determined diagnostic values of species based on uniform numerical criteria applied in a comprehensive vegetation-plot database. We assumed an *a priori* diagnostic value for a certain class if a species was listed in DENGLER & BERG (2001) as character species of that class or its subordinate units or as a joint class differential species of that class together with one or two other classes of open (non-woodland) vegetation. We modified these assessments in a few cases where the respective species is very rare or at its distributional margin in Mecklenburg-Vorpommern and we thus deemed the diagnostic values of DENGLER & BERG (2001) as misleading in Hesse, resulting in the *a priori* assignments documented in brackets behind species names in Tables 2 and 3 (in the Supplement). We summed the weighted presences of diagnostic species of each class per relevé, using the ordinal values (OTVs) of the cover-abundance categories, i.e. $r \rightarrow 1$, $+$ $\rightarrow 2$ etc. (VAN DER MAAREL 2007). Each relevé was then assigned to the class with the highest sum, i.e. whose diagnostic species prevailed (DENGLER et al. 2006, MICHL et al. 2010). This assignment and additionally the second-highest ranked class (if it was within 5 OTVs of the first) are indicated in the vegetation table.

Third, we determined diagnostic values within the data set based on the four vegetation classes as delimited according to step 2. We used phi values of association (CHYTRÝ et al. 2002a) for standardised relevé numbers per vegetation unit (see TICHÝ & CHYTRÝ 2006). Species with $\phi \geq 0.5$ were considered as highly diagnostic and those with $\phi \geq 0.25$ as diagnostic (CHYTRÝ 2007b), provided the concentration was significant according to Fisher's exact test at $\alpha = 0.05$. As one *a priori* delimited class of step 2 corresponded to two clusters of step 1, we also determined diagnostic values for the solution with five terminal units.

Fourth, we re-arranged 13 relevés among the five units in cases when diagnostic species (according to step 3) of another unit prevailed over that of the same unit, aiming to increase the distinctness of the classification by raising the phi values of the diagnostic and particularly the highly diagnostic species. Most of the re-arranged relevés had been identified as transitional by the top-down approach (2) and/or had been assigned to the corresponding unit in the cluster approach (1).

Finally, the diagnostic species for the refined classification within the context of nutrient-poor grasslands in the Aar valley were re-determined as in step 3 and the table was vertically arranged according to decreasing phi-values within the species blocks.

3.5 Syntaxonomic assignment and nomenclature

We searched the literature for the appropriate syntaxonomic placement of the vegetation units and their correct names using chiefly KNAPP (1978), OBERDORFER (1993a, 1993b), SCHAMINÉE et al. (1996), BERG et al. (2001, 2004), RENNWALD (2002) and CHYTRÝ (2007a). The syntaxonomic naming follows the International Code of Phytosociological Nomenclature (ICPN; WEBER et al. 2000), adopting its Recommendation 10C (i.e. the addition of epitheta whenever the eponymous taxon is clear) for all hierarchical levels below the class. In cases of pending applications to the *Committee for Nomina Conservanda, Ambigua, Inversa & Mutata* (CNC), we present in Subsection 4.2 both the currently valid name and its suggested replacement, while in the text and in the tables our preferred name is used.

3.6 Statistical analyses

To display the floristic interrelationships between the relevés in a multidimensional space, we carried out a detrended correspondence analysis (DCA) with the same transformed cover values as for the cluster analysis (see Subsection 3.4) in CANOCO 4.5 using down-weighting of rare species in order to avoid undue influence on the outcome (TER BRAAK & ŠMILAUER 2002). In the ordination diagram the relevés were coded according to the refined vegetation units of step 4 in Subsection 3.4. Relationships between the first two DCA axes on the one hand, and floristic and environmental parameters on the other were analysed with Pearson correlations in SPSS 14 (SPSS Inc., Chicago, USA).

Finally, we tested for floristic and environmental differences among the five associations with one-way ANOVAs carried out in SPSS 14. The same was done with the soil parameters from the lab (see Subsection 3.3). We tested whether the prerequisites of the ANOVA models (normal distribution, equal variance) were sufficiently met by visually inspecting the distribution of the residuals (QUINN & KEOUGH 2002). The only variable that showed serious problems were the K^+ concentrations in the B horizon. In this case we therefore re-analysed the data after a log-transformation. When the ANOVA detected a significant pattern, we used Tukey's *post hoc* test at $p < 0.05$ to determine homogeneous groups of associations.

4. Phytosociological classification and syntaxonomy

4.1 General structure

The *a priori* assignment to classes yielded communities from four classes of grasslands, *Calluno-Ulicetea*, *Koelerio-Corynepherea*, *Festuco-Brometea* and *Molinio-Arrhenatheretea*. Due to our focus on nutrient-poor, dry grasslands, the latter class was represented in our data set only by very few relevés transitory to the other classes, despite being frequent in the region. The cluster analysis resulted in four major units, largely corresponding to the finally distinguished associations CU1, CU2, KC and FB (see below), with the first division being between the two *Calluno-Ulicetea* units and all other relevés. The plots that were *a priori* assigned to the *Molinio-Arrhenatheretea* did not form a separate cluster, not on the four-cluster level and neither at higher resolutions; instead they clustered mostly together with the *Koelerio-Corynepherea*. Similarly, the four associations CU1, CU2, KC and FB were well separated on the plane of the first two DCA axes, while the five MA relevés overlapped with the FB and KC clusters (Fig. 7).

The adopted final classification (following the distinctness maximisation described in step 4 in Subsection 3.4 deviated from the cluster analysis apart from the acceptance of MA as a separate unit by reassignment of 17 relevés (3 from CU2 to FB, 9 from KC to FB, 3 from KC to CU2, 1 from FB to CU2, 1 from KC to CU1).

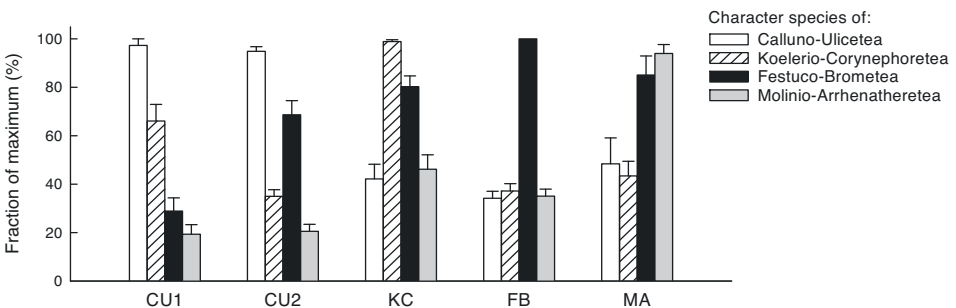


Fig. 3: Fractions of *a priori* diagnostic species of four vegetation classes found in the five grassland associations. Mean values and standard errors are shown. CU1: *Polytricho-Festucetum tenuifoliae/Galio-Deschampsietum flexuosae*, CU2: *Festuco-Genistelletum*, KC: *Jasiono-Festucetum ovinae*, FB: *Gentiano-Koelerietum*, MA: *Arrhenatheretum*.

Abb. 3: Anteile der *a priori*-festgelegten diagnostischen Arten von vier Vegetationsklassen in den Beständen der untersuchten fünf Assoziationen. Mittelwerte und Standardfehler sind dargestellt. Die Bedeutung der Assoziationskürzel kann der englischen Legende entnommen werden.

4.2 Syntaxonomic overview

The five associations distinguished are coded as CU1, CU2, KC, FB and MA throughout the paper. Two alternative syntaxonomic views exist for CU1: While B.N. and E.B. identify CU1 as the *Polytricho piliferi-Festucetum tenuifoliae* to be classified in the alliance *Violion caninae*, J.D. and T.B. prefer to place this association in the alliance *Genistion pilosae*, where J.D. identifies it with the *Galio hircynici-Deschampsietum flexuosae*. In cases of pending applications to the CNC, the proposed name is given first and the one that is still valid but should be replaced for different reasons is given in brackets.

Class *Calluno-Ulicetea* Br.-Bl. & Tx. ex Klika & Hadač 1944

Order *Nardetalia strictae* Preising 1950

Alliance *Violion caninae* Schwickerath 1944

CU1 (first view): *Polytricho piliferi-Festucetum tenuifoliae* R. Knapp 1978

CU2: *Festuco rubrae-Genistelletum sagittalis* Issler 1929

Order *Vaccinio-Genistetalia* Schubert ex Passarge 1964

Alliance *Genistion pilosae* Schwickerath 1944

CU1 (second view): *Galio hircynici-Deschampsietum flexuosae* Passarge 1979

Class *Koelerio-Coryneporetea* Klika in Klika & V. Novák 1941

Order *Trifolio arvensis-Festucetalia ovinae* Moravec 1967

Alliance *Hyperico perforati-Scleranthion perennis* Moravec 1967

KC: *Jasiono montanae-Festucetum ovinae* Klika 1941 nom. invers. propos.

(*Festuco ovinae-Jasionetum montanae* Klika 1941)

Class *Festuco-Brometea* Br.-Bl. & Tx. ex Klika & Hadač 1944

Order *Brachypodietalia pinnati* Korneck 1974

(*Brometalia erecti* W. Koch 1926 nom. amb. propos.)

Alliance *Bromion erecti* W. Koch 1926

FB: *Gentiano-Koelerietum pyramidatae* Knapp ex Bornkamm 1960 nom. cons. propos.

(*Carlino acaulis-Brometum erecti* Oberd. 1957)

Class *Molinio-Arrhenatheretea* Tx. 1937

Order *Arrhenatheretalia elatioris* Tx. 1931

Alliance *Arrhenatherion elatioris* Luquet 1926

MA: *Arrhenatheretum elatioris* Br.-Bl. 1915

4.3 The plant communities (Table 2 and 3)

4.3.1 *Polytricho piliferi-Festucetum tenuifoliae* or *Galio hircynici-Deschampsietum flexuosae*

Characterisation: This relatively species-poor association (23.8 species in 20 m², Fig. 8A) is dominated by *Deschampsia flexuosa* in the herb layer and almost always by *Pleurozium schreberi* in the moss layer. The species with the highest diagnostic value in the local context and in addition to the class character species joined with the *Festuco-Genistelletum* are young plants of *Cytisus scoparius*, as well as *Rumex acetosella* and *Teesdalia nudicaulis*. The other highly frequent species are the grasses *Agrostis capillaris* and *Festuca rubra* agg. as well as the mosses *Ceratodon purpureus* and *Rhytidiadelphus squarrosus*. The plant community is markedly acidophytic and resembles *Nardus* swards (in species composition and structure) but *Nardus stricta* and *Galium saxatile* are almost absent. It is characterized by medium to high cover values of tussock grasses (*Agrostis capillaris*, *Deschampsia flexuosa*, *Festuca filiformis*, *F. rubra* agg.) and mosses (*Brachythecium albicans*, *Ceratodon purpureus*, *Dicranum polysetum*, *D. scoparium*, *Hypnum cupressiforme*, *Rhytidiadelphus squarrosus*, *Scleropodium purum*).

Syntaxonomy: The authors of this paper agree that plant community CU1 matches the class *Calluno-Ulicetea* rather than the *Koelerio-Coryneporetea*. This is supported by the results of the classification and ordination which places the CU1 relevés next to those of the *Festuco-Genistelletum sagittalis* and far from the KC relevés of the *Koelerio-Coryneporetea*. Some of us (B.N., E.B.) would like to assign the *Deschampsia-Festuca-Agrostis*-dominated plant

Table 2: Abbreviated synoptic table of the five associations of nutrient-poor grasslands in the study region, based on the relevé table (Table 3 in the Supplement). The associations are: CU1 = *Polytricho-Festucetum tenuifoliae/Galio-Deschampsietum flexuosae*; CU2 = *Festuco-Genistetum*; KC = *Jasiono-Festucetum ovinae*; FB = *Gentiano-Koelerietum*; MA = *Arrhenatheretum*. Only diagnostic species in the context of the study and other species that exceeded 20% constancy in at least one association are shown. The diagnostic species are arranged according to decreasing phi-values in the regional context at class level (*Calluno-Ulicetea*) or at association level (other five blocks), provided the concentration of a species was significant at $p < 0.05$. Species that are diagnostic for more than one unit are listed under the unit with the higher phi-value. The phi-values are indicated with superscript symbols (**: $\phi > 0.50$; *: $\phi > 0.25$; °: $\phi > 0.00$). Additionally, highly diagnostic species (**) are printed in bold. Diagnostic species of classes are shaded dark grey and those of alliances light grey. In the header, association means for some relevant parameters are given; for more information, see relevé table (Table 3). The *a priori* class assignment as assumed in this study is indicated behind the species names (CU = *Calluno-Ulicetea*; KC = *Koelerio-Corynephoretea*, FB = *Festuco-Brometea*; MA = *Molinio-Arrhenatheretea*; for details, see Methods).

Tabelle 2: Gekürzte Stetigtabelle der Magerrasen des unteren Aartals basierend auf der Vegetations-tabelle (Tabelle 3 in der Beilage). Die Assoziationen sind CU1 = *Polytricho-Festucetum tenuifoliae/Galio-Deschampsietum flexuosae*; CU2 = *Festuco-Genistetum*; KC = *Jasiono-Festucetum ovinae*; FB = *Gentiano-Koelerietum*; MA = *Arrhenatheretum*. Nur diagnostische Arten im Kontext der Arbeit und sonstige Arten mit > 20% Stetigkeit in einer Assoziation wurden dargestellt. Die diagnostischen Arten sind nach fallenden phi-Werten auf Klassenebene (*Calluno-Ulicetea*) bzw. Assoziationsebene (die anderen fünf Artenblöcke) angeordnet, vorausgesetzt die Konzentration der Arten war signifikant mit einer Irrtumswahrscheinlichkeit von $p < 0.05$. Arten, die für mehr als eine Einheit diagnostisch sind, wurden in dem Block mit dem höheren phi-Wert aufgeführt. Die phi-Werte sind durch hochge-stellte Symbole veranschaulicht (**: $\phi > 0.50$; *: $\phi > 0.25$; °: $\phi > 0.00$). Ferner sind hoch-diagnosti-sche Arten (**) fett gedruckt. Diagnostische Arten der Klassen sind dunkelgrau und jene der Verbände hellgrau hinterlegt. Im Tabellenkopf sind Assoziationsmittelwerte für einige relevante Parameter ange-geben (vgl. detaillierte Erläuterung bei der Einzeltabelle, Tabelle 3). Die *a priori*-Klassenzuordnung, welche bei den einzelnen Arten angenommen wurde, ist hinter den Artnamen angegeben (CU = *Callu-no-Ulicetea*; KC = *Koelerio-Corynephoretea*, FB = *Festuco-Brometea*; MA = *Molinio-Arrhenathere-tea*; siehe Text für Details der Methode).

Association	CU1	CU2	KC	FB	MA
Number of relevés	11	25	17	46	5
Calluno-Ulicetea (a priori support; %)	97	95	42	34	48
Koelerio-Corynephoretea (a priori support; %)	66	35	99	37	43
Festuco-Brometea (a priori support; %)	29	69	80	100	85
Molinio-Arrhenatheretea (a priori support; %)	19	21	46	35	94
Cover herb layer (%)	71	71	74	79	92
Cover bryophytes (%)	60	80	37	61	48
Cover lichens (%)	0	1	3	1	0
Species richness (total)	23.6	39.2	44.6	52.4	44.2
Species richness (vascular plants)	16.7	32.6	38.8	46.3	40.4
Species richness (bryophytes)	6.5	6.0	4.7	5.7	3.8
Species richness (lichens)	0.5	0.6	1.1	0.4	0.0
CU – Calluno-Ulicetea					
Deschampsia flexuosa (CU)	100**	96*	12	13	20
Festuca filiformis (CU, KC)	64*	72*	6	2	.
Calluna vulgaris (CU)	36°	72**	.	4	.
Pleurozium schreberi (CU)	91*	100*	18	57°	.
Veronica officinalis (CU)	55°	84*	24	13	20
Dicranum polysetum (CU)	45*	36°	.	17	.
Helictotrichon pratense (FB)	27°	60*	6	15	20
Hypnum jutlandicum (CU)	27*	20°	.	9	.
Polytrichum formosum	27*	16°	6	.	.
Polytrichum piliferum (CU, KC)	18*	8°	.	.	.

Association	CU1	CU2	KC	FB	MA
CU1 – Polytricho-Festucetum tenuifoliae/Galio-Deschampsietum flexuosae					
Cytisus scoparius (juv.)	91**	.	12	11	.
Rumex acetosella (KC)	100**	24	29	11	.
Teesdalia nudicaulis (KC)	55**	8	.	.	.
Carex pilulifera (CU)	36*	4	.	2	.
Senecio sylvaticus	36*	8	.	.	.
Juniperus communis	18*	.	.	.	.
Ranunculus repens (MA)	18*	.	.	.	.
Ceratodon purpureus (KC)	82*	40	76*	24	.
Festuca rubra agg.	100*	64	65	46	80°
Teucrium scorodonia	27*	8	12°	.	.
CU2 – Festuco rubrae-Genistelletum sagittalis					
Genista sagittalis (CU)	.	96**	.	15	20
Potentilla erecta (CU)	.	60**	.	.	20°
Danthonia decumbens (CU)	.	68**	.	46*	.
Hylocomium splendens	9	76**	.	63*	.
Galium pumilum (CU)	9	72*	12	33°	20
Viola canina (CU)	9	76*	.	22	60*
Polygala vulgaris subsp. oxyptera (CU, FB)	9	48*	.	22°	.
Fragaria vesca	9	64*	12	35°	20
Hieracium lachenalii	.	28*	6	4	.
Festuca guestfalica (FB)	9	96*	65°	89*	40
Cladonia ciliata (KC)	.	12*	.	2	.
KC – Koelerio-Corynephoretea: Jasiono-Festucetum ovinae					
Veronica arvensis	.	.	82**	26°	20
Trifolium arvense (KC)	.	8	71**	22°	.
Trifolium campestre (KC, FB)	.	8	76**	35°	.
Trifolium striatum (KC)	.	.	65**	24°	.
Crepis capillaris (MA)	.	.	35**	.	.
Arenaria serpyllifolia (KC)	.	.	59**	28°	.
Hypochaeris radicata (CU, KC)	.	16°	53**	4	.
Bromus hordeaceus	.	.	35**	4	.
Cerastium pumilum (KC)	.	.	41**	11°	.
Potentilla argentea (KC)	.	.	24*	.	.
Draba verna (KC)	9	.	47*	22°	.
Cerastium arvense (KC)	.	4	65*	28°	40°
Myosotis ramosissima (KC)	.	.	41*	26°	.
Thymus pulegioides (FB)	9	60°	94*	91*	20
Aira caryophylla (KC)	.	.	24*	4	.
Trisetum flavescens (MA)	9	20	94*	78°	80°
Brachythecium albicans (KC)	36	12	82*	33	60°
Dianthus deltoides (KC)	18	4	65*	26	40°
Myosotis stricta (KC)	.	4	24*	7	.
Hieracium pilosella (CU, KC, FB)	45	40	88*	65°	40
Plantago lanceolata	18	48	100*	93°	100*
Cladonia foliacea (KC)	.	.	12*	.	.
Cladonia spec.	.	.	12*	.	.
Geranium columbinum	.	.	12*	.	.
Racomitrium canescens agg. (KC)	.	.	12*	.	.
Scleranthus annuus agg.	.	.	12*	.	.
Viola arvensis	.	.	12*	.	.
Vicia angustifolia	.	12	53*	33°	40°
Convolvulus arvensis	.	.	24*	.	20°
FB – Festuco-Brometea: Gentiano-Koelerietum					
Viola hirta	.	.	12	76**	20
Sanguisorba minor (FB)	.	24	41°	98**	40
Linum catharticum (FB)	.	.	.	37**	.
Briza media (FB)	.	24°	.	59*	20

Association	CU1	CU2	KC	FB	MA
<i>Bromus erectus</i> (FB)	.	.	.	26*	.
<i>Agrimonia eupatoria</i>	.	8	29°	70*	40°
<i>Trifolium medium</i>	.	8	.	46*	20°
<i>Centaurea scabiosa</i> (FB)	.	4	29°	48*	.
<i>Koeleria pyramidata</i> (FB)	.	16	6	52*	20°
<i>Astragalus glycyphyllos</i>	.	.	6	28*	.
<i>Plantago media</i> (FB)	.	4	.	41*	20°
<i>Knautia arvensis</i>	.	8	53°	80*	60°
<i>Trifolium alpestre</i>	.	24°	29°	54*	.
<i>Centaurea jacea</i>	.	16	53°	87*	80*
<i>Carex caryophylla</i> (FB)	9	52°	18	72*	20
<i>Brachypodium pinnatum</i> (FB)	.	4	12°	28*	.
<i>Potentilla neumanniana</i> (FB)	36	56°	65°	87*	20
<i>Cirsium acaulon</i> (FB)	.	24°	6	46*	20°
<i>Helictotrichon pubescens</i> (FB, MA)	.	60°	35	85*	80*
<i>Alchemilla glaucescens</i> (FB)	.	.	.	13*	.
<i>Crataegus spec.</i> (juv.)	9	16	24	50*	20
<i>Prunus spinosa</i> (juv.)	9	60°	29	72*	40
<i>Thuidium abietinum</i> (FB)	.	.	.	11*	.
<i>Daucus carota</i> (FB)	.	12	24°	35*	.
<i>Clinopodium vulgare</i>	.	.	24°	37*	20°
<i>Poa angustifolia</i> (FB)	36	36	59°	78*	40
<i>Ononis repens</i> (KC, FB)	9	16	6	39*	20°
<i>Ranunculus bulbosus</i> (FB)	.	16	18	48*	40°
<i>Brachypodium sylvaticum</i>	.	.	6°	15*	.
<i>Medicago lupulina</i> (FB)	.	.	6°	15*	.
<i>Euphrasia stricta</i>	.	4°	.	13*	.
<i>Genista tinctoria</i>	27	80°	41	85*	60°
<i>Lathyrus pratensis</i> (MA)	.	.	6	26*	20°
MA – Molinio-Arrhenatheretea: Arrhenatheretum					
<i>Anthriscus sylvestris</i> (MA)	.	.	.	7	40**
<i>Scorzoneroideis autumnalis</i> (MA)	.	4	.	4	40**
<i>Trifolium repens</i> (MA)	.	12	82*	70°	100*
<i>Valeriana officinalis</i> agg.	.	.	.	17°	40*
<i>Campanula rotundifolia</i> (CU, FB)	45	72°	24	52	100*
<i>Deschampsia cespitosa</i> (MA)	.	.	.	.	20*
<i>Hieracium sabaudum</i>	.	.	.	.	20*
<i>Stellaria alsine</i>	.	.	.	.	20*
<i>Trifolium aureum</i>	.	.	.	.	20*
<i>Vicia sepium</i>	.	.	.	.	20*
<i>Stellaria graminea</i> (CU, MA)	18	12	29°	9	60*
Other graminoid species					
<i>Agrostis capillaris</i> (CU, KC)	100°	84	100°	76	100°
<i>Luzula campestris</i> (CU)	73	100°	76	83°	80
<i>Arrhenatherum elatius</i>	9	64°	53	89°	100°
<i>Anthoxanthum odoratum</i>	18	64°	24	54°	60°
<i>Dactylis glomerata</i>	.	.	53°	70°	80°
<i>Poa pratensis</i> (MA)	36°	4	53°	17	60°
<i>Holcus lanatus</i> (MA)	36°	8	6	30°	60°
<i>Agrostis gigantea</i>	.	28°	6	33°	40°
<i>Elymus repens</i>	.	.	12°	7	20°
<i>Alopecurus pratensis</i> (MA)	.	.	12°	4	20°
<i>Phleum pratense</i> (MA)	.	.	12°	2	20°
<i>Phleum bertolonii</i>	.	.	12°	.	20°
<i>Festuca pratensis</i> (MA)	.	.	.	9°	20°
<i>Carex hirta</i>	.	.	.	2	20°

Association	CU1	CU2	KC	FB	MA
Other forb species					
Pimpinella saxifraga (FB)	27	96°	100°	100°	100°
Achillea millefolium agg.	18	84°	88°	98°	100°
Galium verum (KC, FB)	27	84°	71	87°	100°
Lotus corniculatus (FB)	.	68°	71°	98°	100°
Galium album	27	28	65°	43	80°
Cerastium holosteoides (MA)	27	20	65°	54°	60°
Rumex acetosa (MA)	.	52°	6	48°	80°
Veronica chamaedrys	9	44°	18	52°	60°
Hypericum perforatum	.	16	53°	52°	20
Vicia hirsuta	.	8	47°	41°	40°
Campanula rapunculus	.	8	41°	37°	40°
Trifolium dubium (MA)	.	12	35°	22	40°
Hieracium laevigatum	.	32°	24°	9	40°
Viola riviniana	18	40°	6	17	20
Trifolium pratense (MA)	.	8	18	35°	40°
Leucanthemum ircutianum (FB, MA)	.	8	12	37°	40°
Leontodon hispidus (FB)	.	20°	6	26°	40°
Saxifraga granulata (KC)	.	8	6	28°	40°
Vicia tetrasperma	.	.	24°	13	40°
Senecio jacobaea (FB)	.	12	35°	26°	.
Taraxacum sect. Ruderalia (MA)	.	12	18°	17°	20°
Helianthemum nummularium (FB)	9°	8	6	22°	.
Taraxacum sect. Erythrosperma (KC, FB)	.	.	18°	7	20°
Malva moschata	.	.	12°	13°	20°
Arabidopsis thaliana	.	.	12°	13°	20°
Campanula patula (MA)	.	.	12°	7	20°
Primula veris (FB)	.	.	.	13°	20°
Vicia cracca (MA)	.	.	.	9°	20°
Heracleum sphondylium (MA)	.	.	.	9°	20°
Alchemilla monticola (MA)	.	.	.	9°	20°
Rubus fruticosus agg. et corylifolius agg.	18°	.	6°	4	.
Euphrasia officinalis subsp. rostkoviana	.	12°	12°	4	.
Hypericum maculatum	.	.	.	7°	20°
Colchicum autumnale (MA)	.	.	.	7°	20°
Ranunculus acris (MA)	.	4	.	2	20°
Valerianella locusta (KC)	.	.	18°	7°	.
Rhinanthus minor (MA)	.	4	6°	13°	.
Sedum maximum	.	.	.	2	20°
Other tree and shrub species					
Quercus spec. (juv.)	36	56°	12	46°	40°
Rosa spec. (juv.)	27	40°	53°	39°	20
Prunus domestica (juv.)	.	4	6	4	20°
Pinus sylvestris (juv.)	9°	4	.	11°	.
Other bryophyte species					
Rhytidiadelphus squarrosus (MA)	91°	80	76	91°	100°
Scleropodium purum	73°	72°	24	76°	60
Plagiomnium affine	36	48	53°	61°	60°
Brachythecium rutabulum	27°	4	18	15	40°
Hypnum cupressiforme (CU, KC, FB)	45°	12	24°	22°	.
Dicranum scoparium (CU, KC)	18	32°	24°	17	.
Polytrichum juniperinum (KC)	9	24°	18°	7	.
Climacium dendroides	.	.	6	13°	20°
Thuidium philibertii (FB)	.	.	.	13°	20°
Rhodobryum roseum (KC, FB)	.	12°	12°	9°	.
Calliergonella cuspidata	.	.	.	9°	20°
Other lichen species					
Cladonia furcata (KC)	18°	20°	35°	15	.
Cladonia pyxidata subsp. chlorophaea (CU, KC, FB)	9°	12°	12°	4	.
Cladonia rangiformis (KC)	9°	4	12°	7°	.



Fig. 4: Stand of the *Polytricho piliferi-Festucetum tenuifoliae*/*Galio hircynici-Deschampsietum flexuosae* in the nature reserve „Wacholderheide bei Abrdt“. *Deschampsia flexuosa*-grasslands with *Galium saxatile* (white) and *Calluna vulgaris* (in the foreground) are partly overgrown by *Cytisus scoparius*. In the background the Aar dam lake is visible. (Photo: T. Becker, 2009)

Abb. 4: *Polytricho-Festucetum tenuifoliae*/*Galio-Deschampsietum flexuosae* im Naturschutzgebiet „Wacholderheide bei Abrdt“. Zu sehen ist ein von *Deschampsia flexuosa*-dominierter Bestand mit *Galium saxatile* (weiß) und *Calluna vulgaris* (im Vordergrund) der teilweise von *Cytisus scoparius* überwachsen wird. Im Hintergrund ist der Aarstausee sichtbar. (Foto: T. Becker, 2009)

community to the *Nardetalia*, comprising chiefly acidic grasslands, as opposed to the *Vaccinio-Genistetalia*, mostly dominated by low shrubs. In contrast, J.D. and T.B. prefer an assignment based on purely floristic criteria and supported *inter alia* by the comprehensive Mecklenburg-Vorpommern data set (BERG 2001, 2004). According to this, six species in our relevés would support the *Vaccinio-Genistetalia*/*Genistion pilosae* (*Rumex acetosella* 100%, *Pleurozium schreberi* 91%, *Cytisus scoparius* 91%, *Teesdalia nudicaulis* 55%, *Dicranum polysetum* 45%, *Polytrichum piliferum* 18%), but only two would support the *Nardetalia strictae*/*Violion caninae* (*Luzula campestris* 73%, *Galium saxatile* 9%). Within the *Genistion pilosae*, the stands match the central association *Galio hircynici-Deschampsietum flexuosae* floristically, physiognomically and ecologically as described for instance, from Mecklenburg-Vorpommern (BERG 2004). B.N. and E.B. consider the Mecklenburg-Vorpommern data set of limited validity and credibility for the phytosociological interpretation and compositional statistics of plant communities in the German siliceous uplands. E.B. and B.N. identify our association as the *Polytricho piliferi-Festucetum tenuifoliae*, as described by KNAPP (1978) with 19 relevés from Middle Hesse, and lectotypified by GREGOR (2001). KNAPP (1978) distinguished three subassociations (*typicum*, *cladonietosum*, *thymetosum pulegioidis*), with the latter being transitory to the *Diantho deltoidis-Festucetum tenuifoliae* R. Knapp 1978. Both associations, specified as dry tussock grasslands („*Horst-Trockenrasen*“) by KNAPP (1978), were referred to as widespread („*sehr verbreitet*“) in the Taunus and Lahn-Dill Highlands, and plentiful („*reichlich*“) in the Wetterau. Almost all his relevés of the *Polytricho-Festucetum tenuifoliae* were recorded in the Wetterau and the Taunus foothills, between 160 and 430 m a.s.l. Our relevés resemble his *Polytricho-Festucetum*

tenuifoliae stands particularly in the high constancy of *Deschampsia flexuosa*, regarded by KNAPP (1978) as a special drought-resistant ecotype. The rather late flowering *Agrostis vinealis* (= *A. coarctata*), a frequent component in KNAPP's (1978) *Polytricho piliferi-Festucetum tenuifoliae* and largely missing in our relevés, may have been overlooked in some of our plots. KNAPP (1978) did not assign the *Polytricho-Festucetum tenuifoliae* to any higher-rank syntaxon but J.D. and T.B. conclude that he excluded the *Violion caninae* as the appropriate alliance by stating "in higher altitudes the *Polytricho-Festucetum* will be displaced by *Nardus stricta* grasslands" („Diese acidophilen Trockenrasen werden in höheren Gebirgslagen zunehmend durch ... Borstgras-Rasen ... ersetzt"). DENGLER (2004) considers the *Polytricho-Festucetum tenuifoliae* a younger synonym of the *Galio veri-Festucetum capillatae* Br.-Bl. & de Leeuw 1936 nom. invers. et mut. propos., thereby widening the scope of the *Festuco capillatae-Galietum maritimi* Br.-Bl. & de Leeuw 1936, an association described from stabilized coastal dunes, to comprise also inland swards with *Festuca filiformis* (= *F. capillata*, *F. tenuifolia*) and to be placed in the *Sedo-Cerastion arvensis* Sissingh & Tideman 1960 (*Koelerio-Corynephoretea*). B.N. and E.B. do not accept the synonymisation of the *Polytricho piliferi-Festucetum tenuifoliae* with the *Festuco capillatae-Galietum maritimi* under the "roof" of the emended *Galio veri-Festucetum capillatae*, as the coastal grasslands with *Carex arenaria* and *Corynephorus canescens* and other psammophytes differ considerably from the *Polytricho-Festucetum tenuifoliae* of the siliceous uplands.

Distribution: This community seems to be limited to the eastern part of the study area. The relevés originate from the plateau of the Wörlberg north of Mittenaar-Offenbach and from the adjacent sites *Wildestein* and *Königsköppel*. Furthermore, the association occurs in the nature reserve "Wacholderheide bei Abdrt" near the Aar dam lake and some other places in the Lahn-Dill Mountains. The wider range of the *Polytricho-Festucetum tenuifoliae* (as delimited by B.N. and E.B.) cannot be specified at present, as it was only rarely recorded in phytosociological studies. In contrast, the *Galio-Deschampsietum flexuosae* (as delimited by J.D.) is a widespread vegetation type in many regions of temperate and northern Europe with acidic substrata, but probably due to its low floristic attractiveness it has only rarely been treated in syntaxonomic overviews.

4.3.2 *Festuco rubrae-Genistelletum sagittalis*

Characterisation: This moderately species-rich association (39.9 species on 20 m², Fig. 8A) is in the herb layer jointly dominated by *Calluna vulgaris*, *Deschampsia flexuosa*, *Festuca filiformis*, *F. geystfalica*, *F. rubra* agg. and *Helictotrichon pratense*, while *Hylocomium splendens*, *Pleurozium schreberi* and *Rhytidiadelphus squarrosus* dominate the well-developed moss layer. In addition to the class character species shared with the first association, the species with the highest diagnostic value in the local context are *Genista sagittalis*, *Potentilla erecta*, *Danthonia decumbens* and *Hylocomium splendens*, the latter two being also frequent in the *Gentiano-Koelerietum agrostietosum tenuis*. Other highly frequent species are *Achillea millefolium* agg., *Agrostis capillaris*, *Galium verum*, *Genista tinctoria*, *Luzula campestris*, *Pimpinella saxifraga* and *Veronica officinalis*. Our records confirm KNAPP's (1978) observation according to which the *Festuco-Genistelletum* occurs mostly under drier conditions than the *Nardus*-rich swards of the *Polygalo vulgaris-Nardetum strictae* which also occurs in the Lahn-Dill Highlands.

Syntaxonomy: This plant community is widely accepted within the *Violion caninae* as an association separate from the *Polygalo vulgaris-Nardetum strictae* (Preising 1953) Oberd. 1957 nom. cons. propos. (e.g. KNAPP 1978, OBERDORFER 1978, POTT 1995, PEPPLER-LISBACH & PETERSEN 2001, SCHUBERT et al. 2001). The *Festuco-Genistelletum* differs from the *Polygalo-Nardetum*, *inter alia*, in the highly frequent association character species *Genista sagittalis* (= *Genistella sagittalis* = *Chamaespartium sagittale*), and the rarity of *Nardus stricta* (which occurred only once with "+" in our relevés). Nevertheless, WEDRA (1990) and RENNWALD (2002) combine both units (and several others) into one association, which would bear the oldest valid name *Festuco-Genistelletum* (s.l.); this concept is preferred by



Fig. 5: Detail of a *Festuco rubrae*-*Genistelletum sagittalis* stand. *Genista sagittalis* and *Galium pumilum* are flowering. (Photo: B. Nowak, 1985)

Abb. 5: Detail eines *Festuco rubrae*-*Genistelletum sagittalis*-Bestandes mit *Genista sagittalis* und *Galium pumilum* in Blüte. (Foto: B. Nowak, 1985)

one of us (B.N.). The stands in our study area show clear relationships towards the class *Festuco-Brometea* (which also becomes evident in Fig. 3), with high constancy of species such as *Helictotrichon pratense*, *Potentilla neumanniana*, *Carex caryophyllea*, *Sanguisorba minor* and *Cirsium acaulon*. They correspond to the *Aveno-Genistelletum* Oberd. 1957, which according to OBERDORFER (1978: p. 229) might be considered a geographic race of the *Festuco-Genistelletum*. We agree with PEPPLER-LISBACH & PETERSEN (2001) who identify stands like ours as *Festuco-Genistelletum avenetosum pratensis* (Oberd. 1957) Manz 1990.

Distribution: In the Lahn-Dill Highlands, *Genista sagittalis*, the formative species of this association, is found only around Ballersbach and Bicken (LÖBER 1950). Similar grasslands without *Genista sagittalis* occur widely on diabase, basalt and baserich shale substrates in western and central Hesse. In the study area, this association is limited to the south-west part. It occurs mainly west of Mittenaar-Ballersbach near the village's sports area and at the sites *Niederbachsberg* and *Hainberg* (scattered at the last site). The *Festuco-Genistelletum* was recorded in Middle Hesse in the southern and western Taunus (five relevés between 460 and 600 m a.s.l. from KNAPP 1978, and two relevés in WEDRA 1990). The Taunus stands seem to be less species-rich than in our study area, more pronouncedly acidophytic, and *Genista sagittalis* generally prevails. The association has a subatlantic-submediterranean distribution (OBERDORFER 1978). The stands of the Lahn-Dill Highlands are the northeasternmost of the association ever recorded.

4.3.3 *Jasiono montanae-Festucetum ovinae*

Characterisation: This fairly species-rich association (44.9 species on 20 m², Fig. 8A) is in the herb layer jointly dominated by *Agrostis capillaris*, *F. guestfalica*, *F. rubra* agg. and *Hieracium pilosella*, while *Brachytecium albicans* dominates the moss layer. The species with the highest diagnostic value in the local context are *Veronica arvensis*, *Trifolium arvense*, *T. campestre*, *T. striatum*, *Crepis capillaris*, *Arenaria serpyllifolia*, *Hypochaeris radicata*, *Bromus hordeaceus* and *Cerastium pumilum*. Other highly frequent species are *Luzula campestris*, *Pimpinella saxifraga*, *Plantago lanceolata*, *Thymus pulegioides*, *Trifolium repens* and *Trisetum flavescens*. Our records and others from the Lahn-Dill Highlands near our study area (BERGMEIER 1987) reveal plant assemblages of numerous perennial herbs and grasses, including, e.g., *Campanula rapunculus*, *Centaurea jacea*, *Cerastium arvense*, *Dianthus deltoides*, *Galium verum*, *Hypericum perforatum*, *Hypochaeris radicata*, *Jasione montana*, *Knautia arvensis*, *Lotus corniculatus* and *Vicia angustifolia*. Apart from *B. albicans*, the mosses *Ceratodon purpureus*, *Plagiomnium affine*, *Polytrichum juniperinum* and *Rhytidiadelphus squarrosus* were frequently recorded. The *Jasiono montanae-Festucetum ovinae* includes stands transitory to *Nardetalia* communities (KNAPP 1978: „Variante von *Viola canina*“; GREGOR 2001: „Variante mit *Calluna vulgaris*“), stands with considerable proportions of *Arrhenatheretalia* species (SCHMITT & FARTMANN 2006), and – in our relevés as well as in KNAPP (1978) – open swards with numerous annuals such as *Aira caryophyllea*, *Draba verna*, *Myosotis discolor*, *M. ramosissima*, *M. stricta*, *Scleranthus polycarpus*, *Trifolium arvense*, *T. campestre*, *T. striatum* and *Veronica arvensis*. In fact, among the communities studied, the *Jasiono-Festucetum ovinae* displays the highest proportion of vascular therophytes and a highest coverage of lichens (2.9% on average) (Table 4).

Syntaxonomy: Acidophilous meso-xeric grasslands dominated by various fescue species (*Festuca ovina* agg. and *Festuca rubra* agg.) have been treated in different classes in the syntaxonomic literature of Central Europe. They were partly placed within the *Festuco-*



Fig. 6: Detail of a *Jasiono montanae-Festucetum ovinae* stand. *Trifolium striatum* and *Genista tinctoria* are flowering. (Photo: B. Nowak, 1985)

Abb. 6: Detail eines *Jasiono montanae-Festucetum ovinae*-Bestand mit *Trifolium striatum* und *Genista tinctoria* in Blüte. (Foto: B. Nowak, 1985)

Brometea (*Koelerio-Phlegetalia phleoidis* Korneck 1974, *Koelerio-Phleion phleoidis* Korneck 1974; e.g. KORNECK 1974, OBERDORFER 1993a, POTT 1995, CHYTRÝ 2007a), and partly within the *Koelerio-Corynephoretea* (MORAVEC 1967, KRAUSCH 1968, POTT 1995, SCHAMINÉE et al. 1996, BERG et al. 2001, 2004, CHYTRÝ 2007a), partly even in the *Calluno-Ulicetea* (*Violion caninae*; e.g. the *Campanulo rotundifoliae-Dianthetum deltoidis* Balátová-Tuláčková 1980; JANIŠOVÁ 2007, ŠKODOVÁ et al. 2011). For plant communities within the *Koelerio-Corynephoretea*, two solutions have been suggested, either the assignment to a widely delimited order *Sedo acris-Festucetalia* Tx. 1951 nom. invers. propos. (including the subcontinental to continental xeric grasslands of the *Koelerion glaucae* Volk 1931) (e.g. POTT 1995, SCHUBERT et al. 2001), or to the order *Trifolio-Festucetalia ovinae* (e.g. MORAVEC 1967, SCHAMINÉE et al. 1996, BERG et al. 2004). DENGLER (2003) demonstrated that it is more convincing on floristic and synchorological grounds to separate the *Trifolio-Festucetalia ovinae* from the *Sedo acris-Festucetalia* s.str. According to this concept, the *Trifolio-Festucetalia ovinae* are widespread meso-xeric fescue grasslands with more or less closed swards on sandy or other siliceous soils with moderately acidic to neutral soil reaction, analogous to the meso-xeric grasslands of the order *Brachypodietalia pinnati* on calcareous soils. The subdivision of the *Trifolio-Festucetalia ovinae* into alliances is still poorly understood; we follow here the preliminary proposal of DENGLER (2001, 2004), who distinguished three alliances in Central, Western and Northern Europe: *Armerion elongatae* Pötsch 1962 (subcontinental Pleistocene sands, dominated by *Festuca brevipila*), *Hyperico-Scleranthion* Moravec 1967 (siliceous soils in the uplands, dominated chiefly by *F. ovina*, *F. guestphalica* or others) and *Sedo-Cerastion arvensis* Sissingh & Tideman 1960 (sandy and siliceous soils in atlantic-subatlantic regions, dominated mainly by *F. filiformis*). While our plant community clearly belongs to the second alliance, the taxonomy of this association has been very inconsistent. To our knowledge, *Festuco ovinae-Jasionetum montanae* Klika 1941, described from Central Bohemia, Czech Republic (KLIKA 1941), is the oldest valid and thus the correct name for the association. CHYTRÝ (2007a) also applied this name for the Czech stands. As both in the holotypus and in practically all stands of this association, *Festuca ovina* agg. prevails over *Jasione montana*, we follow CHYTRÝ's (2007a) proposal to reverse the name sequence according to Art. 42 ICPN to *Jasiono montanae-Festucetum ovinae*. Plant species assemblages similar to ours have been termed *Thymo pulegioidis-Festucetum ovinae* Oberdorfer 1957, *Jasiono montanae-Dianthetum deltoidis* Oberdorfer ex Mucina in Mucina et al. 1993, *Diantho deltoides-Festucetum tenuifoliae* R. Knapp 1978, *Cerastio arvensis-Agrostietum pusillae* Moravec 1967, *Diantho deltoidis-Galietum veri* Toman 1977 and *Pimpinella saxifraga-Festuca ovina*-[*Plantagini-Festucion*] community sensu RENNWALD (2002). DENGLER (2004: 315), under the name *Thymo pulegioidis-Festucetum ovinae*, listed altogether 26(!) synonyms for our association. GREGOR (2001) provided a nomenclatural review for numerous association names of sheep fescue grasslands. While in our relevés from the Aar valley, therophytes such as *Aira caryophyllea*, *Draba verna* or *Scleranthus annuus* agg. play only a subordinate role and succulents are practically absent, in other parts of the Lahn-Dill Highlands *Koelerio-Corynephoretea* stands with more pioneer-like character occur (BERGMEIER 1987, TEUBER 1998), which belong to the orders *Thero-Airetalia* Rivas-Goday 1964 and *Sedo-Scleranthetalia* Br.-Bl. 1955. However, the nutrient-poor grasslands described by OTTE et al. (2008) under the name *Airo caryophylleae-Festucetum ovinae* Tx. 1955 nom. inval. from the nature reserve "Kanzelstein bei Eibach" rather belongs to the *Jasiono-Festucetum ovinae*.

Distribution: In the study area, the *Jasiono-Festucetum ovinae* has two distribution centres, both of them north of the Aar river. The eastern centre includes the south face of the *Wörbelberg* north of Mittenaar-Offenbach and the *Sandberg* north of Bischoffen. In contrast, the western distribution centre is in the surroundings of Herborn-Seelbach where the association can be found at the sites *Bornberg*, *Forstkopf* and *Horchberg*. In the Lahn-Dill Highlands this association used to be common on former fields with nutrient-poor soil. In Middle, East and North Hesse the *Jasiono-Festucetum ovinae* was recorded under various

names by KNAPP (1978, *Diantho-Festucetum tenuifoliae*), HÜLBUSCH et al. (1982, *Galium verum-Dianthus deltoides*[*Armerion elongatae*]-Gesellschaft), GLAVAC (1983) and BERGMEIER (1987, *Festuca rubra-Agrostis tenuis*-[*Arrhenatheretalia*]-Gesellschaft), BÖNSEL & SCHMIDT (1991), GREGOR (2001, as *Heidenelken-Rotschwingel-Rasen*) and – in the Hesse-Westphalia borderline area – by SCHMITT & FARTMANN (2006, *Thymo pulegioidis-Festucetum ovinae*). The wider distribution of the association is not well-known, but it appears to be widespread throughout the Hercynian Highlands and occurs sporadically in the lowlands around the Baltic Sea (OBERDORFER 1957, DENGLE 2004, CHYTRÝ 2007a).

4.3.4 *Gentiano-Koelerietum pyramidatae*

Characterisation: This very species-rich association (53.1 species on 20 m², Fig. 8A) is typically dominated in our data by *Festuca guestfalica*, with *Brachypodium pinnatum*, *Bromus erectus* and *Koeleria pyramidata* being co-dominants in some stands. Among the herbs the highest cover values are reached by *Cirsium acaulon*, *Hieracium pilosella* and *Trifolium alpestre*. The moss layer is jointly dominated by *Hylocomium splendens*, *Rhytidiadelphus squarrosus* and *Scleropodium purum*. Species with the highest diagnostic value in the local context are *Viola hirta*, *Sanguisorba minor* and *Linum catharticum*, further diagnostic species are *Agrimonia eupatoria*, *Centaurea scabiosa*, *Koeleria pyramidata*, *Plantago media* and *Trifolium medium*. Other highly frequent species are *Achillea millefolium* agg., *Agrostis capillaris*, *Arrhenatherum elatius*, *Centaurea jacea*, *Galium verum*, *Genista tinctoria*, *Helictotrichon pubescens*, *Knautia arvensis*, *Lotus corniculatus*, *Luzula campestris*, *Pimpinella saxifraga*, *Plantago lanceolata*, *Potentilla neumanniana*, *Thymus pulegioides* and *Trisetum flavescens*. Similar stands in Middle Hesse have been characterized additionally by combinations of species including *Danthonia decumbens*, *Festuca filiformis*, *Galium pumilum*, *Helic-*



Fig. 7: Nutrient-poor siliceous grassland on diabase (*Gentiano-Koelerietum pyramidatae* agrostietosum). *Saxifraga granulata* (white) and *Potentilla neumanniana* (yellow) are flowering. (Photo: C. Schmiede, 1994)

Abb. 7: Kalkmagerrasen auf Diabas (*Gentiano-Koelerietum pyramidatae* agrostietosum). *Saxifraga granulata* (weiß) und *Potentilla neumanniana* (gelb) blühen. (Foto: C. Schmiede, 1994)

totrichon pratense, *Hypochaeris radicata*, *Ononis repens*, *Polygala vulgaris*, *Ranunculus bulbosus*, *Saxifraga granulata* and *Spiranthes spiralis* (KORNECK 1960, KNAPP 1978, BERGMEIER 1987, BAUMGART 1990). Our data include a few relevés with *Calliergonella cuspidata* und *Colchicum autumnale* associated with temporarily moist soils. The stands with *Bromus erectus* dominance may indicate decreasing and insufficient grazing pressure or abandonment.

Syntaxonomy: While this association is perhaps the best-known plant community of meso-xeric (“semi-dry”) basiphilous grasslands in Central Europe, its subassociation with acidophytes, as represented in our study area, has received much less attention. While most overviews treat the association under the name *Gentiano-Koelerietum* (e.g. OBERDORFER 1993a, SCHAMINÉE et al. 1996, SCHUBERT et al. 2001), *Carlino acaulis-Brometum erecti* Oberd. 1957 is actually an older valid name (RENNWALD 2002, CHYTRÝ 2007a) and thus would be the correct name according to ICPN. As the former is by far the most widely used name, we support the application of RENNWALD (2002) to establish *Gentiano-Koelerietum* as *nomen conservandum* according to Art. 52 ICPN. The association belongs to the subatlantic-submediterranean alliance *Bromion erecti* (often found under the younger syntaxonomic synonym *Meso-Bromion erecti* Oberd. 1949) within the order *Brachypodietalia pinnati* (= *Brometalia erecti* W. Koch 1926 nom. ambig. propos., see DENGLER et al. 2003), which combines the meso-xeric syntaxa of the class across Europe (MUCINA & KOLBEK 1993, DENGLER 2003, 2004). The subassociation with acidophytes as in our study area has been referred to as *Gentiano-Koelerietum agrostietosum tenuis* (Korneck 1960) Oberdorfer & Korneck 1978 or *Gentiano-Koelerietum luzuletosum campestris* (R. Knapp 1958) R. Knapp 1978. The basionym of the former combination is the *Mesobrometum agrostidetosum tenuis* Korneck 1960, described by 12 relevés from the Taunus and near Ortenberg (Wetterau) (KORNECK 1960); the latter combination corresponds to the *Mesobrometum luzuletosum campestris* (KNAPP 1958). For the validity of the name *Festuco-Brometea* in KLIKA & HADAČ (1944), see DENGLER et al. (2012).

Distribution: The *Gentiano-Koelerietum* occurs in the west and north parts of the study area. Here, it was found at the *Blätterwand* site north-west of Offenbach and the *Zaubach* site west of Uebernthal. However, the association occurred most frequently around Herborn-Seelbach, where relevés were taken at the sites *Bornberg*, *Forstkopf*, *Horchberg* and *Hainberg*. Moreover the *Gentiano-Koelerietum* was recorded west (*Niederbachsberg*) and east (*Hemberg*) Mittenaar-Ballersbach. The subassociation of the *Gentiano-Koelerietum* differentiated by acidophytes such as *Agrostis capillaris*, *Danthonia decumbens*, *Hylocomium splendens*, *Luzula campestris* and *Pleurozium schreberi* was recorded from the Taunus foreland, the Wetterau, the Gladenbacher Bergland, Vogelsberg, Kuppenrhön and Westerwald (KORNECK 1960, OBERDORFER & KORNECK 1978, KNAPP 1978, BERGMEIER 1987, WEDRA 1990), moreover in some parts of SW Germany (OBERDORFER & KORNECK 1978). Most stands occur between 250 and 400 m a.s.l. The *Gentiano-Koelerietum* as a whole is known from SW Germany (northeastwards to S Lower Saxony, W Saxony-Anhalt, Thuringia and parts of Bavaria), Austria, Switzerland, E France, Belgium, Luxembourg and S Netherlands (e.g. ZOLLER 1954, OBERDORFER 1993a, SCHAMINÉE et al. 1996, JANDT 1999, SCHNEIDER 2011), while stands reported under the name *Carlino-Brometum* from Czechia (CHYTRÝ 2007a) have a transitional character towards the subcontinental alliance *Cirsio-Brachypodion pinnati* Hadač & Klika in Klika & Hadač 1944 (for the validity of this name, see DENGLER et al. 2012).

4.3.5 *Arrhenatheretum elatioris*

Characterisation: This subtype of the *Arrhenatheretum* on nutrient poor and slightly dry sites is fairly species-rich (44.6 species on 20 m², Fig. 8A). It is typically co-dominated by the grass species *Agrostis capillaris*, *Arrhenatherum elatius*, *Festuca rubra* agg., *Helictotrichon pubescens* and *Holcus lanatus*. The only highly diagnostic species in the local context are *Anthriscus sylvestris* and *Scorzoneroideis autumnalis*, followed by *Trifolium repens*, *Valeriana officinalis* agg. and *Campanula rotundifolia*. As the first two have low frequency and

Table 4: Characteristics of the five nutrient-poor grassland associations in the lower Aar valley. Means and standard errors are given. Different letters indicate significant differences between communities at $p < 0.05$ from Tukey test. EIV = Ellenberg indicator value, UIV = utilization indicator value. Note, that the presented significance levels of EIV/UIV comparisons between communities should not be taken at face value because Type I error rates are inflated due to the non-independence of the values.

Tabelle 4: Eigenschaften der fünf Magerrasengesellschaften im unteren Aartal. Mittelwerte und Standardfehler sind dargestellt. Werte mit unterschiedlichen Buchstaben unterscheiden sich signifikant bei $p < 0,05$ nach dem Tukey-Test. EIV = Ellenberg-Zeigerwert, UIV = Nutzungs-Zeigerwert. Beachte, dass die Signifikanzwerte der EIV/UIV-Vergleiche nicht überbewertet werden dürfen, da die Variablen voneinander abhängig und die Typ-I-Fehlerrate daher in einer einfachen Varianzanalyse unterschätzt wird.

	<i>Polytricho-Festucetum tenuifoliae/Galio-Deschampsietum flexuosae</i>	<i>Festuco-Genistetum</i>	<i>Jasione-Festucetum ovinae</i>	<i>Gentiano-Koelerietum</i>	<i>Arrhenatheretum</i>	<i>p from ANOVA</i>
Number of relevés	11	25	17	46	5	–
Elevation (m a. s. l.)	328 ± 12	324 ± 5	305 ± 7	308 ± 5	316 ± 25	0.175
Slope (°)	4.8 ± 1.6 ^b	9.4 ± 1.4 ^{ab}	11.9 ± 1.5 ^{ab}	13.6 ± 1.1 ^a	12.4 ± 2.7 ^{ab}	0.003
Heat load index	0.84 ± 0.01 ^b	0.82 ± 0.01 ^b	0.95 ± 0.01 ^a	0.89 ± 0.01 ^{ab}	0.90 ± 0.04 ^{ab}	< 0.001
EIV for temperature	4.7 ± 0.07 ^b	4.9 ± 0.05 ^b	5.5 ± 0.07 ^a	5.3 ± 0.03 ^a	5.3 ± 0.05 ^a	< 0.001
EIV for moisture	4.1 ± 0.07 ^b	4.2 ± 0.03 ^b	3.9 ± 0.06 ^b	4.1 ± 0.03 ^b	4.5 ± 0.04 ^a	< 0.001
EIV for soil reaction	3.8 ± 0.08 ^c	4.6 ± 0.09 ^b	5.5 ± 0.13 ^a	5.9 ± 0.07 ^a	5.7 ± 0.20 ^a	< 0.001
EIV for nutrients	3.2 ± 0.13 ^b	3.0 ± 0.06 ^b	3.4 ± 0.10 ^b	3.4 ± 0.06 ^b	4.0 ± 0.15 ^a	< 0.001
UIV for trampling tolerance	5.0 ± 0.13 ^a	4.6 ± 0.06 ^b	4.8 ± 0.07 ^{ab}	4.6 ± 0.03 ^b	4.6 ± 0.07 ^b	< 0.001
UIV for cutting tolerance	5.4 ± 0.08 ^{ab}	4.9 ± 0.07 ^c	5.5 ± 0.10 ^a	5.1 ± 0.04 ^{bc}	5.6 ± 0.18 ^a	< 0.001
UIV for grazing tolerance	5.0 ± 0.08 ^a	4.5 ± 0.04 ^c	4.8 ± 0.08 ^{ab}	4.6 ± 0.03 ^{bc}	4.6 ± 0.07 ^{bc}	< 0.001
UIV for fodder quality	4.2 ± 0.09 ^{cd}	4.0 ± 0.08 ^d	4.7 ± 0.09 ^{ab}	4.4 ± 0.04 ^{bc}	5.0 ± 0.15 ^a	< 0.001
Height of upper herb layer (cm)	61 ± 4.4 ^{ab}	73 ± 2.3 ^{ab}	57 ± 5.7 ^b	82 ± 3.6 ^a	78 ± 12.8 ^{ab}	< 0.001
Cover of herb layer (%)	71 ± 4.5 ^b	71 ± 2.6 ^b	74 ± 3.2 ^b	79 ± 1.8 ^{ab}	92 ± 2.2 ^a	0.004
Cover of bryophytes (%)	60 ± 5.7 ^{ab}	80 ± 3.2 ^a	37 ± 7.1 ^b	61 ± 4.0 ^{ab}	48 ± 12.3 ^b	< 0.001
Cover of lichens (%)	0.0 ± 0.0	0.6 ± 0.4	2.9 ± 2.4	0.6 ± 0.3	0.0 ± 0.0	0.318
Species richness (total)	23.8 ± 1.6 ^c	39.9 ± 1.7 ^b	44.9 ± 2.1 ^{ab}	53.1 ± 1.4 ^a	44.6 ± 5.9 ^{ab}	< 0.001
Species richness (herbs)	14.7 ± 1.4 ^c	30.7 ± 1.5 ^b	37.4 ± 2.1 ^{ab}	43.8 ± 1.3 ^a	39.0 ± 4.3 ^{ab}	< 0.001
Species richness (woody species)	2.0 ± 0.3 ^{ab}	1.9 ± 0.2 ^{ab}	1.4 ± 0.2 ^b	2.5 ± 0.2 ^a	1.4 ± 0.7 ^{ab}	0.020
Species richness (bryophytes)	6.5 ± 0.6	6.0 ± 0.5	4.7 ± 0.8	5.7 ± 0.3	3.8 ± 1.0	0.104
Species richness (lichens)	0.5 ± 0.3	0.6 ± 0.2	1.1 ± 0.4	0.4 ± 0.1	0.0 ± 0.0	0.181

cover, the more important diagnostic feature is the rarity of characteristic species of the three other grassland classes. Other highly frequent species are *Achillea millefolium* agg., *Centaurea jacea*, *Dactylis glomerata*, *Galium verum*, *Lotus corniculatus*, *Luzula campestris*, *Pimpinella saxifraga*, *Plantago lanceolata*, *Rhynchospora squarrosus* and *Trisetum flavescens*.

Syntaxonomy: The division of the *Arrhenatherion* into associations is still under debate – DIERSCHKE (1997) accepts one association and four informal communities, while ELLMAUER & MUCINA (1993) present seven associations and one informal community for Austria, CHYTRÝ (2007a) four associations for Czechia, and JANIŠOVÁ (2007) five associations for Slovakia. We leave this to a supra-national analysis based on a comprehensive data set and consistent methodology, and apply here the oldest association name available in the alliance. Whether or not the evaluation of CHYTRÝ (2007a) was correct that the name *Arrhenatherion elatioris* W. Koch 1926 is invalid according to Art. 7 ICPN (Koch [1926] does not provide a relevé himself but refers to the publication “Scherrer 1925”), according to Art. 33 ICPN CHYTRÝ’s choice among two homonyms of equal age is binding. Within the *Arrhenatheretum* s.l. numerous subassociations have been described (DIERSCHKE 1997). As a large-scale overview at association level is missing, we refrain from a formal assignment of our stands. It can be said that they belong to the subassociation group of *Briza media* (DIERSCHKE 1997), which is characteristic for nutrient-poor, moist to slightly drier sites. In the regional context, they have been attributed to the subassociation *hypochaeridetosum radicatae* Lisbach et Pepler-Lisbach 1996 (OTTE et al. 2008). If more narrowly delimited associations are accepted, our stands likely would belong to the *Ranunculo bulbosi-Arrhenatheretum elatioris* Ellmauer in Ellmauer & Mucina 1993, the *Poo-Trisetetum flavescens* R. Knapp ex Oberd. 1957, or the *Anthoxantho odorati-Agrostietum flavescens* Sillinger 1933 (see CHYTRÝ 2007a, JANIŠOVÁ 2007, ŠKODOVÁ et al. 2011).

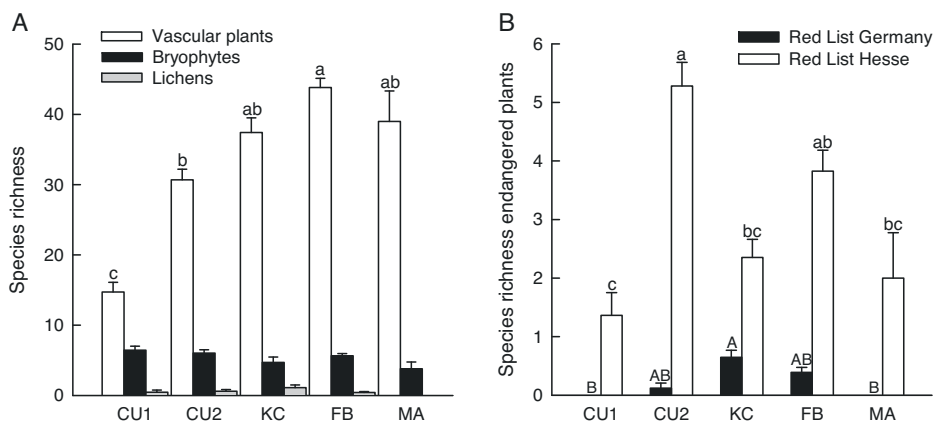


Fig. 8: Richness of all species (A; divided into herbaceous vascular plants, bryophytes and lichens), and of endangered vascular plant species (B; divided into national and state level; including those of the Near Threatened list) found in the plots (mostly 20 m²) of five nutrient-poor grassland associations in the lower Aar valley. Mean values and standard errors are shown. Values with different letters differ significantly at $p < 0.05$. CU1: *Polytricho-Festucetum tenuifoliae/Galio-Deschampsietum flexuosae*, CU2: *Festuco-Genistetum*, KC: *Jasiono-Festucetum ovinae*, FB: *Gentiano-Koelerietum*, MA: *Arrhenatheretum*.

Abb. 8: Artenreichtum (A; weiß: Gefäßpflanzen ohne Gehölzjungwuchs; schwarz: Moose; grau: Flechten) und gefährdeten Pflanzenarten (B; inkl. Vorwarnliste; schwarz: Deutschland; weiß: Hessen) in fünf Magerrasengesellschaften im unteren Aartal. Mittelwerte und Standardfehler sind dargestellt. Werte mit unterschiedlichen Buchstaben unterscheiden sich signifikant bei $p < 0,05$. Die Bedeutung der Assoziationskürzel kann der englischen Legende entnommen werden.

Distribution: According to our focus on low-growing grasslands, this association is under-represented in our data set considering its actual frequency in the study area. The few relevés originate from the area south of Herborn-Seelbach and around Mittenaar-Offenbach. Within the Lahn-Dill Highlands low-input and species-rich *Arrhenatheretum* grasslands belong to the predominant vegetation units (NOWAK 1990). The widely circumscribed association is widespread in temperate Europe.

5. Vegetation-environment relationships

5.1 Gradient analysis

In the ordination diagram the associations CU1+CU2 were clearly separated from the associations KC+FB along the first axis, while along the second axis CU1+KC were separated from CU2+FB (Fig. 9). The few relevés assigned to MA did not constitute a distinct group within the ordination plane. The first axis of the DCA was positively correlated with the EIV for soil reaction. The EIVs for temperature and nutrients and the head load index corroborate that KC and FB occur on drier and warmer sites with less acidic soils containing more nutrients (Table 6). Moreover, the first DCA axis was positively correlated with the fodder quality and cover and richness of herbs, which suggests that KC and FB offer more favourable conditions and yield better fodder. The second axis was positively correlated with EIV for soil reaction (but less strongly than axis 1), and negatively to the four utility values, namely (in declining order) those for cutting, grazing and trampling tolerance, as well as fodder quality. EIV for moisture was correlated neither to the first nor to the second DCA axis. Note that significance levels of EIV/UIV correlations should not be taken at face value because due to the non-independence of the variables, the actual error probabilities are normally higher than those calculated with Pearson correlations.

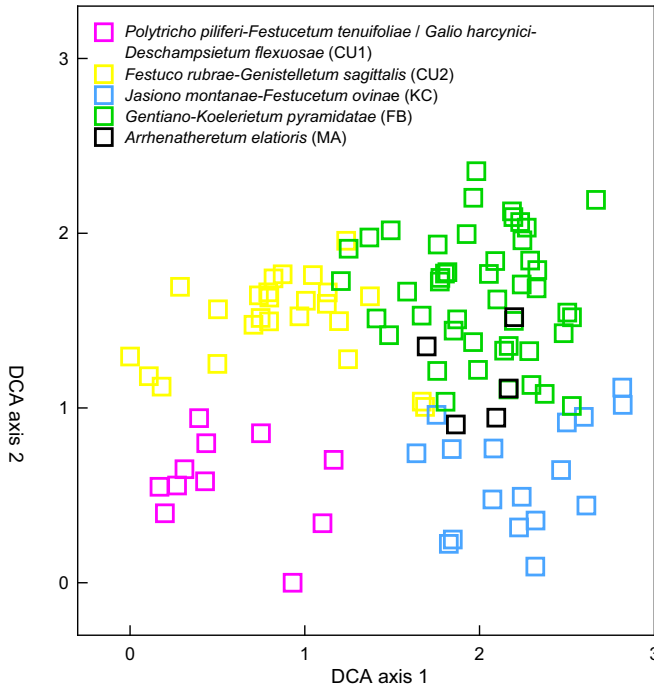


Fig. 9: Gradient analysis (DCA) of the nutrient-poor siliceous grasslands in the lower Aar valley. 104 samples, 261 species. Eigenvalue axis 1: 0.339, axis 2: 0.189.

Abb. 9: Gradientenanalyse (DCA) der Silikatmagerrasen des unteren Aartals. 104 Aufnahmen, 261 Arten. Eigenwert Achse 1: 0.339, Achse 2: 0.189.

Table 5: Pearson correlations between two DCA axes and environmental variables. Arrows indicate positive (↑) or negative (↓) correlations. Note, that significance levels of EIV/UIV correlations should not be taken at face value because due to the non-independence of the variables, the actual error probabilities are normally higher than those calculated with Pearson correlations.

Tabelle 5: Zusammenhänge zwischen den ersten beiden Achsen nach einer DCA und Umweltvariablen. Dargestellt sind Pearson-Koeffizienten. Die Pfeile geben an, ob eine Korrelation positiv (↑) oder negativ (↓) ist. Man beachte, dass die Signifikanzwerte der Pearson-Korrelationen mit den Zeigerwerten nicht überbewertet werden sollten, da die Variablen voneinander abhängig sind und Pearson-Korrelationen daher die tatsächlichen Typ-I-Fehlerraten unterschätzen.

	DCA axis 1		DCA axis 2	
	r^2	p	r^2	p
Elevation	0.05 ↓	0.020	0.00 ↑	0.967
Slope	0.12 ↑	< 0.001	0.06 ↑	0.014
Head load	0.21 ↑	< 0.000	0.04 ↓	0.036
EIV for temperature	0.60 ↑	< 0.001	0.00 ↑	0.857
EIV for moisture	0.01 ↓	0.288	0.03 ↑	0.073
EIV for soil reaction	0.79 ↑	< 0.001	0.20 ↑	< 0.001
EIV for nutrients	0.33 ↑	< 0.001	0.02 ↓	0.198
UIV for trampling tolerance	0.02 ↓	0.165	0.15 ↓	< 0.001
UIV for cutting tolerance	0.10 ↑	0.001	0.42 ↓	< 0.001
UIV for grazing tolerance	0.00 ↓	0.576	0.25 ↓	< 0.001
UIV for fodder quality	0.38 ↑	< 0.001	0.09 ↓	0.002
Height of upper herb layer	0.02 ↑	0.135	0.17 ↑	< 0.001
Cover of herb layer	0.17 ↑	< 0.001	0.01 ↑	0.316
Cover of bryophytes	0.14 ↓	< 0.001	0.12 ↑	< 0.001
Cover of lichens	0.00 ↓	0.755	0.01 ↓	0.292
Species richness (herbs)	0.56 ↑	< 0.001	0.16 ↑	< 0.001
Species richness (bryophytes)	0.08 ↓	0.004	0.01 ↑	0.391
Species richness (lichens)	0.02 ↓	0.208	0.04 ↓	0.056

5.2 Soil conditions

The results of the soil investigations show that the three associations CU1, CU2 and FB occur on shallow and penetrable soil (Fig. 10). Total soil depth (normally until bedrock) tended to be highest in CU1 and lowest in FB. Consequently the effective root penetration depth and the effective field capacity tended to be higher in CU1 and lower in FB (Table 6). In total, water capacity of the soil was low in all three associations.

The pH of the Ah horizon measured in water was highest in FB and lowest in CU1 with the CU2 values lying in between (Fig. 10). The same pattern (with slightly higher values) was observed in the pH of the B horizon and (with slightly lower values) in the pH measured in KCl. Base saturation of the Ah horizon in FB was significantly higher than in CU2. In CU1 the base saturation of the soil was very low. In CU2 and FB the base saturation was higher in the B horizon than in the Ah horizon, and the other way around in CU1. The potential cation exchange capacity (CEC_{pot}) in the Ah horizon of FB was significantly higher than in both CU1 and CU2. The same order of the associations was found (with lower values of the cation exchange capacity) in the B horizon. Especially the Ca content of the Ah horizon was very high in FB while it was low in the two other associations. Ca concentrations in the B horizon were surprisingly lower than in the Ah horizon but showed the same pattern between associations. The content of K and Mg in the Ah horizon of FB was also higher than in CU2 and CU1, while the Na content differed minimally between associations. This also held for the C/N ratio of the top soil, which was around 12 in all three associations (Table 6).

Table 6: Soil conditions in three nutrient-poor grassland associations in the lower Aar valley. Mean values and simple standard errors are shown. Values with different letters differ significantly at $p < 0.05$. p values derived from ANOVA.

Tabelle 6: Bodenbedingungen in drei Magerrasengesellschaften im unteren Aartal. Mittelwerte und einfache Standardfehler sind dargestellt. Werte mit unterschiedlichen Buchstaben unterscheiden sich signifikant bei $p < 0,05$. Die p -Werte stammen aus Varianzanalysen.

	<i>Polytricho-Festucetum tenuifoliae/ Galio-Deschampsietum flexuosae</i>	<i>Festuco-Genistelletum</i>	<i>Gentiano-Koelerietum</i>	p from ANOVA
	$n = 3$	$n = 8$	$n = 10$	$n = 21$
Root penetration depth (cm)	53 ± 23.5	54 ± 8.4	44 ± 6.6	0.707
Field capacity (mm)	84 ± 39.1	82 ± 13.1	66 ± 9.6	0.618
<i>Ah horizon</i>				
Soil depth (cm)	12.3 ± 1.5	15.5 ± 1.4	14.4 ± 2.3	0.729
pH (H ₂ O)	4.3 ± 0.09 ^c	5.6 ± 0.21 ^b	6.9 ± 0.21 ^a	< 0.001
pH (KCl)	3.8 ± 0.12 ^b	4.5 ± 0.20 ^b	5.8 ± 0.28 ^a	< 0.001
Base saturation (%)	8.2 ± 1.6 ^b	34.6 ± 8.0 ^b	80.6 ± 4.8 ^a	< 0.001
CEC _{pot} (μmol/g)	315 ± 44.7 ^{ab}	266 ± 42.5 ^b	456 ± 28.9 ^a	0.007
Ca ²⁺ (μmol/g)	18 ± 3.1 ^b	45 ± 8.1 ^b	204 ± 21.5 ^a	< 0.001
Na ⁺ (μmol/g)	0.41 ± 0.03	0.47 ± 0.03	0.61 ± 0.07	0.137
K ⁺ (μmol/g)	1.71 ± 0.71 ^b	4.18 ± 0.86 ^{ab}	5.33 ± 0.37 ^a	0.020
Mg ²⁺ (μmol/g)	5.1 ± 0.9	59.4 ± 43.5	104.3 ± 37.2	0.395
C/N ratio	12.0 ± 0.9	12.1 ± 0.3	12.0 ± 0.6	0.989
N (g/100 g)	0.57 ± 0.12	0.39 ± 0.04	0.43 ± 0.04	0.158
Organic matter (%)	14.0 ± 3.25	9.5 ± 1.29	10.4 ± 0.98	0.211
<i>Bv horizon</i>				
Soil depth (cm)	41 ± 22.1	31 ± 6.6	22 ± 5.3	0.341
pH (H ₂ O)	4.8 ± 0.10 ^a	6.0 ± 0.22 ^a	7.4 ± 0.33 ^a	< 0.001
pH (KCl)	4.1 ± 0.03 ^b	4.7 ± 0.21 ^{ab}	6.0 ± 0.39 ^a	0.006
Base saturation (%)	7.8 ± 1.6 ^c	41.7 ± 8.4 ^b	85.7 ± 4.3 ^a	< 0.001
CEC _{pot} (μmol/g)	146 ± 11.0 ^b	203 ± 42.2 ^b	406 ± 42.0 ^a	0.003
Ca ²⁺ (μmol/g)	8 ± 1.2 ^b	42 ± 8.2 ^b	169 ± 19.4 ^a	< 0.001
Na ⁺ (μmol/g)	0.36 ± 0.04	0.51 ± 0.04	0.72 ± 0.11	0.056
K ⁺ (μmol/g)	0.44 ± 0.06 ^b	1.40 ± 0.35 ^{ab}	2.06 ± 0.28 ^a	0.032
Mg ²⁺ (μmol/g)	2.0 ± 0.3	61.0 ± 42.2	106.3 ± 47.9	0.449
C/N ratio	9.0 ± 0.9	8.7 ± 0.5	19.3 ± 5.3	0.127
N (g/100 g)	0.24 ± 0.04	0.18 ± 0.02	0.19 ± 0.03	0.519
Organic matter (%)	4.4 ± 1.06	3.2 ± 0.50	5.4 ± 0.69	0.067

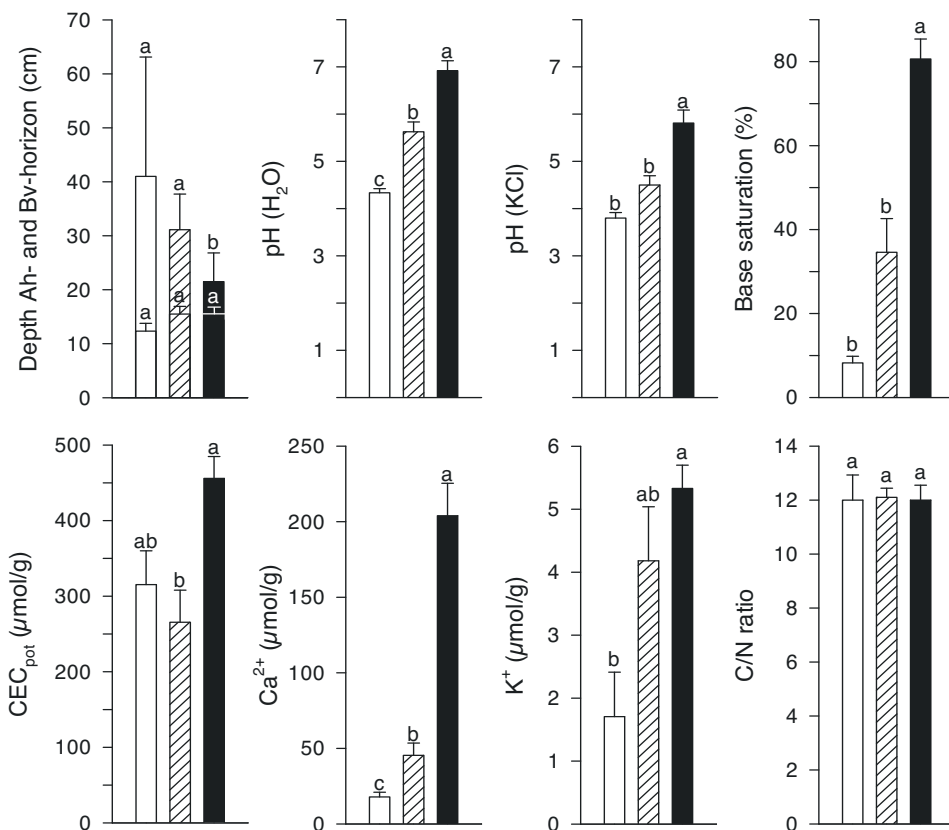


Fig. 10: Soil conditions in the Ah horizon of the *Polytricho-Festucetum tenuifoliae*/*Galio-Deschampsietum flexuosae* (white bars; $n = 3$), *Festuco-Genistelletum* (striped bars; $n = 8$) and *Gentiano-Koelerietum* (black bars; $n = 10$) in the lower Aar valley. Mean values and standard errors are shown. Values with different letters differ significantly at $p < 0.05$. (see also Table 6)

Abb. 10: Bodenbedingungen im Ah-Horizont des *Polytricho-Festucetum tenuifoliae*/*Galio-Deschampsietum flexuosae* (weiße Balken; $n = 3$), *Festuco-Genistelletum* (gestreifte Balken; $n = 8$) und *Gentiano-Koelerietum* (schwarze Balken; $n = 10$) im unteren Aartal. Mittelwerte und einfache Standardfehler sind dargestellt. Werte mit unterschiedlichen Buchstaben unterscheiden sich signifikant bei $p < 0,05$. (s. Tabelle 6)

6. General discussion and outlook

6.1 Environmental effects

In our study, species composition (and thus community differentiation) was mainly affected by variables related to the acidity of the soil. Soil acidity affects important ecosystem properties e.g. soil fertility (by the rate of decomposition of organic matter) and form of available nitrogen (NH_4^+ or NO_3^-) (ELLENBERG & LEUSCHNER 2010). However, it also determines richness and composition of grasslands due to the relatively higher number of basiphilous compared to acidophilous species (CHYTRÝ et al. 2003, TYLER 2003, BECKER et al. 2007). The pH amplitude of our stands covers the border between acid and basic conditions (indicated by an unusual mixture of basiphilous and acidophilous species) and therefore matches the position where community differentiation is strongly affected by the pH. In contrast, water availability, otherwise known as a key ecological factor in dry grasslands (e.g. BECKER et al. 2011), was less important in our study because our habitats were generally semi-dry.

The correlation between the indicator value for temperature and both species composition and richness can be considered an artefact: Many of the acidophilous species (on one end of the DCA axis) are widespread in both higher altitudes and latitudes and therefore categorised as psychrophilic. In general, indicator values should be treated with caution when correlating them with DCA axes or testing for differences between floristically defined vegetation units because variables are not independent (ZELENÝ & SCHAFFERS in press).

Our stands of the *Jasiono-Festucetum ovinae* often grow on former arable land that was abandoned in the 1960s to 1970s. This was indicated by the common occurrence of many therophytes and lower numbers of endangered plant species (at least after the Hesse Red List) than in the older stands of the *Festuco-Genistelletum* and *Gentiano-Koelerietum* dating back to medieval times. Endangered plant species in grasslands often show low colonisation capacity due to low dispersal potential and/or specific environmental requirements of these plants, and therefore are often absent from young grasslands (RUPRECHT 2005, WAESCH & BECKER 2009). However, nutrient-poor grasslands may also contain endangered plant species as indicated by the high frequency of *Trifolium striatum* in our stands. Overall, the stands of the *Jasiono-Festucetum ovinae* mostly represent persistent successional stages of *Bromion erecti* and *Violion caninae* grasslands, which may evolve after decades of thorough grazing.

6.2 Classification methodology

In this study, we applied several complementary classification techniques in an iterative manner. The result was a classification that fitted both into supra-regional classification schemes and gave floristically clearly defined associations in the regional context. Moreover, four of the five associations were extremely well delimited (i.e. with no overlaps) on the first two ordination axes (see Fig. 9). Would our overall approach thus be suitable for other studies too, what are its advantages and where are potential weaknesses?

First of all, our approach is only meant for studies with a geographically and/or syntaxonically strongly limited data set. In such situations, a purely numerical approach, based solely on the relevés in the study (as our cluster analysis), is able to find some of the major floristic patterns in this data set, but the match with supra-regionally established systems is low. In particular, most numerical approaches often overlook units represented by only few relevés and they tend to create units of similar size (see review in DENGLER 2003). In our case, the cluster analysis “overlooked” the few *Molinio-Arrhenatheretea* relevés and assigned fewer relevés to the *Gentiano-Koelerietum* than justified by the species composition. However, creating such an idiosyncratic classification (as that based on cluster analysis) would make it impossible to benefit from all the knowledge about floristic composition, ecology, distribution, succession, management and conservation that is connected to the syntaxon names (DENGLER 2003, EWALD 2003, DENGLER et al. 2008). Traditionally, phytosociologists tried to match units in regional studies with published syntaxonomic systems by manual table sorting (DIERSCHKE 1994). However, this approach lacks transparency and repeatability, and is challenged by the fact that in most countries there are several inconsistent classification systems in use.

Using an *a priori* assignment based on long lists of established diagnostic species of higher units has been shown here to produce a very reasonable starting point of the regional classification (as in previous studies by DENGLER et al. 2006, MICHL et al. 2010). Unlike WILLNER (2011), we used the summed OTVs and not the summed percentage cover values to avoid disproportionate effects of a few species that tend to become dominant but which often have no narrow coenological preference (e.g. *Festuca rubra* agg., *Rhynchospora squarrosus*). If there were a general classification system for Germany that provides diagnostic values for all species at all hierarchical levels based on a statistically evaluated comprehensive vegetation database, a top-down approach would achieve a perfect and 100% reproducible assignment of the regional relevés to the national system as indicated by WILLNER (2011). However, presently we only have one syntaxonomic overview with numerically evaluated diagnostic species for all vegetation types in one German region (Mecklenburg-Vorpommern: BERG et

al. 2001, 2004). It is clear that neither all taxa nor all syntaxa occur there, and some are rare or at their distributional limits so that the evaluation from this federal region is not fully transferable to other regions. Therefore, we further refined the community types that were already reasonably well defined after this *a priori* assignment in a next step by maximising the crispness (i.e. phi values of the highly diagnostic species) through moving several relevés between the groups. This was done manually as no computer tool is presently available to carry out this step. This resulted in more clearly delimited units, which, however, kept their close correspondence to the supra-regional system.

Finally, it is worth comparing the *a priori* assignment of diagnostic values (in this case for classes) with the context-dependent diagnostic values achieved in the regional data set. First of all, there is a high overlap (see vegetation table, Table 2), which tells us that the species generally behave similarly in Mecklenburg-Vorpommern and in Hesse. However, there are also notable differences. Some are simply due to the fact that we dealt only with a small fraction of syntaxa in the regional study. Due to the exclusion of forest-edge communities in our study, many *Trifolio-Geranietea sanguinei* species were detected as “diagnostic” for the *Festuco-Brometea* (e.g. *Viola hirta*, *Trifolium medium*, *Astragalus glycyphyllos*). Here the regional diagnostic values would change (and become similar or identical to those from Mecklenburg-Vorpommern) if the class *Trifolio-Geranietea sanguinei* were to have been included in the study. On the other hand, for bryophytes the assessments from our regional study with thorough bryophyte sampling might be more reliable than diagnostic values reported by DENGLER & BERG (2001) or BERG & DENGLER (2005), because in the database of Mecklenburg-Vorpommern the treatment of non-vascular plants is of varying quality and this could only partly be corrected when determining diagnostic values. For example *Hylocomium splendens* was reported as joint diagnostic species of the classes *Oxycocco-Sphagneteta* Br.-Bl. & Tx. ex Westhoff et al. 1946, *Parvo-Caricetea* den Held & Westhoff in Westhoff & den Held 1969 nom. cons. propos., and *Festuco-Brometea* by DENGLER & BERG (2001), but with only 1% constancy in any of these classes, while the present study indicates that this pleurocarpous moss is more likely a joint character species of the *Calluno-Ulicetea* and *Festuco-Brometea*.

6.3 Contributions to large-scale classification and outlook

With this paper, we documented five associations with high-quality relevés (i.e. uniform plot size, thorough treatment of non-vascular plants and of microspecies of *Festuca ovina*). Two of these associations have only very rarely been documented in the German phytosociological literature, although they are presumably relatively widespread (see distribution information in BERG et al. 2004): KC – *Jasiono-Festucetum ovinae* is not included in the two recent syntaxonomic overviews of Germany (POTT 1995, SCHUBERT et al. 2001), either under these names, or – to the best of our knowledge – under any other name, while CU1 – *Polytricho-Festucetum tenuifoliae*/ *Galio-Deschampsietum flexuosae* is missing in the first named reference work. In the checklist of syntaxa in Germany (RENNWALD 2002) these vegetation types are at least included, albeit not as regular associations: *Deschampsia flexuosa*-[*Calluno-Ulicetea*] community and *Pimpinella saxifraga-Festuca ovina*-[*Plantagini-Festucion*] community. Evidently, the widespread ignorance of both community types is related to the fact that they have no association character species, but are negatively characterised central associations of their alliances (e.g. BERG et al. 2004), combined with the common perception among phytosociologists that only stands with association character species are worth recording (reviewed and criticized in GLAVAC 1996, DENGLER 2003, EWALD 2003). However, there is no objective justification for neglecting such vegetation types: they frequently occur in similar species combinations, cover relevant areas over huge ranges, and they are often also important for conservation (see Subsection 6.4 and BERG et al. 2004). Also the questions raised in Subsection 4.3 whether community type CU1 would better be placed in the *Nardetalia* or in the *Vaccinio-Genistetalia* and how the *Trifolio-Festucetalia ovinae* should best be subdivided in alliances and associations can only be answered when much more data are

available from such “ignored” vegetation types. Luckily, recent large-scale overviews, such as BERG et al. (2004), CHYTRÝ (2007a et seq.), JANIŠOVÁ (2007), or WILLNER & GRABHERR (2007), have overcome this system of differently “valued” community types and now accept all floristically well-separated, widely distributed units as associations.

Our regional study showed that despite the long phytosociological tradition in Germany, there are still gaps where both knowledge and data are missing. While unfortunately, Germany is lacking a comprehensive national vegetation database unlike many of its neighbouring countries (JANSEN et al. 2011, but see EWALD et al. 2010), there are at least some big databases available and growing, which together could offer the basis for a consistent classification of the grassland and other vegetation types of Germany based on the analysis of individual relevés. It would be beneficial to develop numerical classification approaches that unlike present cluster algorithms directly maximise the crispness of the resulting units in terms of phi values. Once such a comprehensive classification is available, floristic definitions of the syntaxa of all levels with statistically determined groups of diagnostic species would be possible. This means an extension of DENGLE & BERG (2001) to the whole of Germany, which then – following the ideas of WILLNER (2011) – could be used in a top-down approach to classify any new relevé based on the prevailing diagnostic species, which could easily be automated.

6.4 Conservation

The nutrient-poor grasslands described here are floristically very species-rich and contain many endangered plant species (Fig. 8B, Table 7). Their “unusual” composition (from a supra-regional point of view), though typical for the Lahn-Dill Highlands, is characterised by the co-occurrence of species from base-rich and acidic dry grasslands on nutrient-poor soil, and makes these habitats particularly worthy of protection. Vulnerable plant species in the grasslands of our study area include *Dianthus deltooides* (CU1, KC, FB, MA), *Genista sagittalis* (mainly CU2), *Teesdalia nudicaulis* (CU1), *Trifolium alpestre* (CU1, KC, FB), *T. striatum* (mainly in KC and FB), as well as *Aira caryophyllea* (mainly KC) and *Danthonia decumbens* (CU2, FB), which are classified as near threatened in Hesse. The local population of *G. sagittalis* is particularly noteworthy in this context because it is isolated from the species’ main range and located at its northernmost range margin. Its maintenance depends on a few small semi-dry grasslands around Ballerbach. For further endangered plants of the Aar valley not included within our data, see GRAFFMANN (2004).

From the legal point of view, the *Polytricho-Festucetum tenuifoliae*, *Festuco-Genistelletum* (with highest density of endangered species; Fig. 8B), *Gentiano-Koelerietum* and *Jasiono-Festucetum ovinae* are protected habitats according to the Federal Nature Conservation Act (§ 30 BNatSchG). Four of the studied associations belong to the habitat types listed in Annex I of the Habitats Directive, and thus must be preserved in a representative degree within Natura 2000 areas: *Polytricho-Festucetum tenuifoliae* and *Festuco-Genistelletum* match the Habitats Directive priority habitat type 6230, the *Gentiano-Koelerietum* as habitat type 6210, and *Arrhenatheretum* stands on nutrient-poor soil are considered habitat type 6510. Judging from its plant species composition, the priority habitat type 6270 includes, among others, the *Jasiono-Festucetum ovinae*.

As relicts of a historic rural landscape characterized by agricultural smallholdings with a farming system that is no longer profitable (HIETEL et al. 2005), the nutrient-poor grasslands of the Aar valley are endangered habitats. All the plant communities described here were once widespread in this region, but have suffered serious decline in recent decades both in the Aar valley and in Germany as a whole. The main reasons for this decline in the study area were afforestation in the 1970s and continuing abandonment or under-grazing. In the year of our investigation, for example, 50 % of the stands did not show signs of any recent utilization (mainly stands of CU2 and FB where richness of endangered plant species was especially high) (Table 8). Nevertheless, 40 % of the stands (especially KC) were still grazed by mobile sheep flocks tended by shepherds, indicating the relevance of private sheep farming within the study area for conservation.

Table 7: Red-listed plant species in five nutrient-poor grassland associations in the lower Aar valley. RL-G = German Red List, RL-H = Red List of Hesse. Red List categories: 2 = endangered, 3 = vulnerable, 3- = regionally less vulnerable, V = pre-warning list. CU1 = *Polytricho-Festucetum tenuifoliae/Galio-Deschampsietum flexuosae*, CU2 = *Festuco-Genistelletum*, KC = *Jasiono-Festucetum ovinae*, FB = *Gentiano-Koelerietum*, MA = *Arrhenatheretum*. Percentage constancies per association are given.

Tabelle 7: Pflanzenarten der Roten Listen in fünf Magerrasengesellschaften im unteren Aartal. RL-G = Rote Liste Deutschland, RL-H = Rote Liste Hessen. Gefährdungskategorie: 2 = stark gefährdet, 3 = gefährdet, -3 = regional schwächer gefährdet, V = Vorwarnliste. Es sind prozentuale Stetigkeiten pro Assoziation dargestellt. Die Bedeutung der Assoziationskürzel kann der englischen Legende entnommen werden.

Red-listed species	RL-G	RL-H	CU1	CU2	KC	FB	MA
Vascular plants							
<i>Aira caryophylla</i>	–	V	–	–	24	4	–
<i>Alchemilla glaucescens</i>	3	V	–	–	–	13	–
<i>Arnica montana</i>	3	2	–	4	–	–	–
<i>Betonica officinalis</i>	–	V	–	4	–	–	–
<i>Cirsium acaulon</i>	–	V	–	24	6	46	20
<i>Danthonia decumbens</i>	–	V	–	68	–	46	–
<i>Dianthus deltoides</i>	–	V	18	4	65	26	40
<i>Euphrasia officinalis</i> subsp. <i>rostkoviana</i>	–	3	–	12	12	4	–
<i>Euphrasia stricta</i>	–	V	–	4	–	13	–
<i>Galium pumilum</i>	–	V	9	72	12	33	20
<i>Genista germanica</i>	–	3	–	4	–	–	–
<i>Genista sagittalis</i>	–	3	–	96	–	15	20
<i>Helianthemum nummularium</i>	–	V	9	8	6	22	–
<i>Helictotrichon pratensis</i>	–	V	27	60	6	15	20
<i>Myosotis discolor</i>	3	V	–	–	–	2	–
<i>Nardus stricta</i>	–	V	–	4	–	–	–
<i>Platanthera bifolia</i>	3-	3	–	8	–	–	–
<i>Polygala vulgaris</i> subsp. <i>oxyptera</i>	–	V	9	48	–	22	–
<i>Primula veris</i>	–	V	–	–	–	13	20
<i>Scabiosa columbaria</i>	–	V	–	–	–	7	–
<i>Scleranthus perennis</i>	–	V	–	–	12	2	–
<i>Teesdalia nudicaulis</i>	–	3	55	8	–	–	–
<i>Trifolium alpestre</i>	–	V	–	24	29	54	–
<i>Trifolium striatum</i>	3	3	–	–	65	24	–
<i>Viola canina</i>	–	V	9	76	–	22	60
Bryophytes and lichens							
<i>Aulacomnium palustre</i>	V	–	9	–	–	–	–
<i>Cladonia arbuscula</i>	3	–	–	8	–	–	–
<i>Cladonia ciliata</i>	3	3	–	12	–	2	–
<i>Cladonia foliacea</i>	3	2	–	–	12	–	–
<i>Cladonia ramulosa</i>	3	3	–	–	–	2	–
<i>Cladonia rangiformis</i>	3	–	9	4	12	7	–
<i>Cladonia scabriuscula</i>	G	G	9	–	6	–	–
<i>Peltigera canina</i>	3	2	–	–	6	–	–
<i>Peltigera polydactylon</i>	3	3	–	–	–	2	–
<i>Peltigera praetextata</i>	3	–	–	–	6	–	–
<i>Peltigera rufescens</i>	3	3	–	–	6	2	–
<i>Racomitrium canescens</i> agg.	V	–	–	–	12	–	–
<i>Rhodobryum roseum</i>	V	–	–	12	12	9	–
<i>Rhytidium rugosum</i>	3	–	–	–	12	4	–
<i>Thuidium abietinum</i>	V	–	–	–	–	11	–

Table 8: Proportions (in %; based on the vegetation plots) of four land use types for the five associations in 1994. CU1 = *Polytricho-Festucetum tenuifoliae*/*Galio-Deschampsietum flexuosae*, CU2 = *Festuco-Genistelletum*, KC = *Jasiono-Festucetum ovinae*, FB = *Gentiano-Koelerietum*, MA = *Arrhenatheretum*.

Tabelle 8: Prozentanteile von vier Landnutzungstypen für die fünf Assoziationen im Jahr 1994. Die Bedeutung der Assoziationskürzel kann der englischen Legende entnommen werden.

	CU1	CU2	KC	FB	MA
Common pasture (<i>Triftweide</i> ; C)	82	16	71	33	20
Fenced pasture (<i>Standweide</i> ; P)	0	4	12	0	0
Hay meadow (M)	0	0	5	11	40
Fallow (F)	18	80	12	56	40

In combination with higher atmospheric N depositions, abandonment and under-grazing has led to creeping eutrophication and scrub colonisation of large areas (cf. DUPRÉ et al. 2010). Grasslands that have not suffered from scrub encroachment but have been occasionally under-grazed changed in species composition towards species-poor *Arrhenatherum* fallows (observation by B.N.). Less common in the study area is the decline of nutrient-poor grasslands due to intensification of land use, for example by fencing to create permanent cattle and horse pasture. In this case, species-poor, mesotrophic *Festuca rubra* pastures (*Arrhenatheretalia*) established (observation by B.N.).

Some of the extant nutrient-poor grasslands are situated within protected areas (Natura 2000 sites or nature reserves). However, in the absence of sufficient management, the survival of even these stands is not guaranteed (as for other grassland types in the area which are highly worthy of protection e.g. species-rich stands of *Arrhenatherion*, *Calthion* and *Molinion*). Deficient funding for maintenance and the shortage of farmers who could perform the necessary grazing render the protection of these habitats difficult. Within our study area, it is mainly due to a few sheep farmers that nutrient-poor pastures have survived the last few decades (observation by B.N.). These farmers graze extensive grasslands with their relatively large flocks without paying rent, but often they ignore the most nutrient-poor grasslands as more nutritious grazing is available elsewhere. For small stands of nutrient-poor grassland of conservation interest, conservation management through ecological compensation laws requiring long-term management plans may be an adequate solution. However, overall, further decline of nutrient-poor grasslands must be expected, with the small areas of the *Polytricho-Festucetum tenuifoliae* and *Festuco-Genistelletum* threatened with extinction in the Lahn-Dill Highlands.

Maintenance of all communities of nutrient-poor grasslands within our study area would be best ensured by further low-intensity common pasturing with sheep. The sheep flocks already available in the area are a good start, but long-term financial incentives for maintaining appropriate grazing pressure on these and other nutrient-poor sites must be available, in combination with raising awareness among farmers of the necessary management. In order to maintain grasslands in good conservation status, several visits with the flock are needed per year. The first grazing period should take place at the beginning of May (at the latest). The vegetation must be cropped short at least twice per year in order to suppress tussock-forming grasses and other competitors such as woody plants. Furthermore, nitrogen must be continually removed, which can be only ensured when sheep are folded overnight outside the grasslands. Moreover, regular additional maintenance is necessary such as removal of pasture weeds and woody plants.

Cutting with removal of hay can be an alternative to grazing. However, this can lead to significant shifts in plant and animal community composition in areas that were previously grazed, as well as to changes in population sizes of individual species and elimination of dwarf shrubs (SCHUHMACHER et al. 1995). If mowing is the only option, it should be performed around mid-June, with a second cut generally not being necessary.

Author contribution statement and acknowledgements

C.S. sampled the vegetation, conducted soil analysis, and analysed data preliminary in her *Diplom* thesis. T.B. initiated and coordinated the writing of the publication, prepared the bottom-up classification and ordination, analysed the vegetation-environment relationships and contributed text in all chapters, while J.D. prepared the top-down classification and contributed major parts of the methods section and the methodological discussion. Community description and phytosociological assignment were mainly done by E.B. and J.D., while B.N. prepared most parts of the sections on grassland history and conservation. All authors critically revised the full text.

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Appendix 1: German grid coordinates of the vegetation plots. Plot numbers correspond to sequential numbers in Table 3.

Appendix 1: Gauß-Krüger-Koordinaten der Aufnahmeflächen. Die Aufnahmeummern entsprechen den laufenden Nummern in Tabelle 3.

No.	x (m/10)	y (m/10)	No.	x (m/10)	y (m/10)	No.	x (m/10)	y (m/10)
1	345922	561880	36	345390	561603	71	345413	561791
2	345958	561922	37	345933	561873	72	345412	561751
3	345878	562008	38	345476	561849	73	345273	561718
4	346248	561815	39	345905	561864	74	345454	561877
5	346250	561810	40	345896	561860	75	345301	561926
6	345877	562002	41	345873	561906	76	345797	561946
7	346246	561806	42	346084	562005	77	345790	561937
8	346240	561805	43	345925	561870	78	345798	561932
9	345927	561882	44	345652	561668	79	345496	561846
10	345976	561906	45	345414	561784	80	345653	561665
11	345920	561898	46	345262	561861	81	345650	561663
12	345454	561526	47	345908	561861	82	345294	561923
13	345456	561524	48	346075	562006	83	345202	561776
14	345396	561633	49	345286	561875	84	345338	561743
15	345446	561521	50	345299	561905	85	345333	561752
16	345466	561571	51	345195	561873	86	345199	561878
17	345460	561548	52	345263	561881	87	345850	561978
18	345451	561511	53	345484	561859	88	345288	561890
19	345447	561513	54	345356	561605	89	345308	561926
20	345464	561565	55	345338	561615	90	345453	561872
21	345447	561524	56	345404	561647	91	345282	561892
22	345466	561567	57	345396	561764	92	345492	561856
23	345391	561613	58	345648	561659	93	346065	562013
24	345466	561562	59	345454	561662	94	345380	561744
25	345464	561558	60	345455	561667	95	345291	561874
26	345460	561559	61	345460	561822	96	345485	561843
27	345449	561528	62	345408	561774	97	345297	561877
28	345454	561520	63	345460	561867	98	345473	561866
29	345412	561654	64	345388	561737	99	345481	561844
30	345394	561630	65	345792	561942	100	345416	561782
31	345448	561517	66	345861	562096	101	345892	562050
32	345396	561617	67	345210	561778	102	345918	561848
33	345416	561751	68	345288	561897	103	345348	561605
34	345406	561724	69	345865	562099	104	345846	561780
35	345402	561613	70	345296	561894			

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Table 3: Vegetation table of the five associations of nutrient-poor grasslands in the study region.

The diagnostic species are arranged according to decreasing phi-values in the regional context at class level (*Calluno-Ulicetea*) or at association level (other five blocks), provided the concentration of a species was significant at $p < 0.05$. Species that are diagnostic for more than one unit are listed under the unit with the higher phi-value. Highly diagnostic species ($\phi > 0.5$) are printed in bold. Left of the species name, the taxonomic/functional groups are indicated (W: woody species except chamaephytes; F: forbs including chamaephytes; G: graminoids; B: bryophytes; L: lichens). In the header, the assignment according to the cluster analysis and the a priori class assignment are indicated; relevés that have finally been classified differently are marked with grey shading. The a priori information used for the diagnostic value of species is indicated after the species name (CU = *Calluno-Ulicetea*; KC = *Koelerio-Coryneporetea*, FB = *Festuco-Brometea*; MA = *Molinio-Arrhenatheretea*). A priori support is expressed as ratio of the cumulative OTVs of the respective class to the maximum value achieved by any of the four classes. Land use is classified as follows: C = common pasture, P = permanent pasture, M = meadow, F = fallow.

Tab. 3: Vegetationstabelle der fünf Assoziationen von Magerrasen im Untersuchungsgebiet.

Die diagnostischen Arten sind nach fallenden phi-Werten auf Klassenebene (*Calluno-Ulicetea*) bzw. Assoziationsebene (die anderen fünf Artenblöcke) angeordnet, vorausgesetzt die Konzentration der Arten war signifikant mit einer Irrtumswahrscheinlichkeit von $p < 0.05$. Arten, die für mehr als eine Einheit diagnostisch sind, wurden in dem Block mit dem höheren phi-Wert aufgeführt. Hoch-diagnostische Arten ($\phi > 0.5$) sind fett gedruckt. Links vom Artnamen ist die taxonomische/funktionelle Gruppe angegeben (W: Jungwuchs von Sträuchern und Bäumen; F: Kräuter und Zwergsträucher; G: Grasartige; B: Moose; L: Flechten). In den Kopfzeilen sind auch die Zuordnung der Aufnahmen nach der Cluster-Analyse und nach der a-priori-Klassenzuordnung angegeben; Aufnahmen, die letztendlich abweichend davon einsortiert wurden sind grau hinterlegt. Die a-priori-Information, welche bei den einzelnen Arten angenommen wurde, ist nach den Artnamen in Klammern angegeben (CU = *Calluno-Ulicetea*; KC = *Koelerio-Corynephoretea*; FB = *Festuco-Brometea*; MA = *Molinio-Arrhenatheretea*). Die a-priori-Unterstützung für die Zuordnung einer bestimmten Aufnahme zu einer Klasse wurde in den Kopfzeilen ausgedrückt als Anteil der aufsummierten ordinal transformierten Artmächtigkeiten der diagnostischen Arten der betreffenden Klasse in Relation zum Maximalwert, den eine der vier betrachteten Klassen erzielte. Die Landnutzung wurde wie folgt klassifiziert: C = Hutweide, P = Standweide, M = Wiese (Mahd), F = Brache.

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