

Dry grasslands of the central valleys of the Alps from a European perspective: the example of Ausserberg (Valais, Switzerland)

Jürgen Dengler^{1,2,3,*} , Stefan Widmer¹ , Eline Staubli¹, Manuel Babbi¹, Jamyra Gehler¹, Daniel Hepenstrick^{1,4}, Ariel Bergamini⁴ , Regula Billeter¹, Steffen Boch⁴ , Sven Rohrer¹ & Iwona Dembicz^{5,6} 

Key words: biodiversity,
Brachypodietalia pinnati, dry
grassland, *Festucetalia valesiacae*,
Festuco-Brometea, inner-alpine dry
valley, *Stipo pulcherrimae-Festucetalia*
pallentis, vegetation classification.

Ključne besede: biotska pestrost,
Brachypodietalia pinnati, suha
travišča, *Festucetalia valesiacae*,
Festuco-Brometea, notranja alpska
suha dolina, *Stipo pulcherrimae-*
Festucetalia pallentis, klasifikacija
vegetacije.

Abstract

The upper Rhone valley in the Swiss canton of Valais is one of the driest and most continental of the inner-alpine valleys and harbours a rich xerothermic flora. We studied syntaxonomy and ecology of dry grasslands and their species richness patterns. In 2018 we recorded 28 vegetation plots (10 m^2) and three nested-plot series of 0.0001 to 100 m^2 on the south-facing slopes above the village of Ausserberg. Mean richness of all species ranged from 1.7 on 1 cm^2 to 47.3 on 100 m^2 , with little contribution of bryophytes and lichens. The species-area relationship for total richness closely followed a power function. Modified TWINSPLAN yielded a three-cluster solution, which could easily be matched with three orders of the class *Festuco-Brometea*: *Stipo pulcherrimae-Festucetalia pallentis* (xeric, rocky), *Festucetalia valesiacae* (xeric, non-rocky) and *Brachypodietalia pinnati* (meso-xeric). The subdivision of the xeric types into two orders is new for Swiss dry grasslands, where these types up to now had been joined in a single alliance *Stipo-Poion* within the *Festucetalia valesiacae*.

Izvleček

Zgornja dolina reke Rone v švicarskem kantonu Valais je ena najbolj sušnih in kontinentalnih notranjih alpskih dolin, kjer najdemo bogato kserotermno floro. Tam smo preučevali sintaksonomijo in ekologijo suhih travišč in vzorce njihove vrstne pestrosti. Leta 2018 smo vzorčili 28 vegetacijskih ploskev (10 m^2) in tri serije ugnezdenih ploskev od 0.0001 do 100 m^2 na južnih pobočjih nad vasjo Ausserberg. Povprečna pestrost vseh vrst je bila od 1,7 na površini 1 cm^2 do 47,3 na 100 m^2 , z majhnim prispevkom mahov in lišajev. V primerjavi s podobnimi združbami v drugih delih Evrope so bile preučevane v vseh merilih manj raznolike. Odnos vrst in površine za celotno vrstno pestrost je bil v skladu s potenčno funkcijo. Z modificiranim programom TWINSPLAN smo dobili tri klastre, ki jih lahko razložimo s tremi redovi razreda *Festuco-Brometea*: *Stipo pulcherrimae-Festucetalia pallentis* (kseričen, kamnit), *Festucetalia valesiacae* (kseričen, brez kamenja) in *Brachypodietalia pinnati* (mezo kseričen). Dodatna členitev kseričnih tipov v dva redova je v primeru suhih travišč v Švici nova, kjer so bili do sedaj vsi tipi združeni v zvezi *Stipo-Poion* znatno redu *Festucetalia valesiacae*.

Received: 19. 4. 2019

Accepted: 10. 6. 2019

Coordinating Editor: Orsolya Valkó

1 Vegetation Ecology Group, Institute of Natural Resource Sciences (IUNR), Zurich University of Applied Sciences (ZHAW), Grüentalstr. 14, 8820 Wädenswil, Switzerland. E-mails: juergen.dengler@zhaw.ch, stefan.widmer@zhaw.ch, staubeli@students.zhaw.ch, manuel.babbi@zhaw.ch, jamyra.gehler@zhaw.ch, daniel.hepenstrick@zhaw.ch, regula.billeter@zhaw.ch, sven@hexdesign.ch * Corresponding author.

2 Plant Ecology, Bayreuth Center for Ecology and Environmental Research (BayCEER), University of Bayreuth, Universitätsstr. 30, 95447 Bayreuth, Germany.

3 German Centre for Integrated Biodiversity Research (iDiv) Halle-Jena-Leipzig, Deutscher Platz 5e, 04103 Leipzig, Germany.

4 Research Unit Biodiversity & Conservation Biology, WSL Swiss Federal Research Institute, Zürcherstr. 111, 8903 Birmensdorf, Switzerland. E-mails: ariel.bergamini@wsl.ch, steffen.boch@wsl.ch

5 Botanical Garden Center for Biological Diversity Conservation in Powsin, Polish Academy of Sciences, Prawdziwka St. 2, 02-973 Warsaw, Poland.

6 Department of Plant Ecology and Environmental Conservation, Faculty of Biology, University of Warsaw, Świerk i Wigury St. 101, 02-089 Warsaw, Poland. E-mail: i.dembicz@gmail.com

Introduction

The inner-alpine dry valleys have long attracted the interest of botanists as they harbour species and vegetation types that are quite unusual for the generally rather cool and moist habitats of the Alps, whereas they resemble in many respects the eastern European steppes (Christ 1879, Braun-Blanquet & Richard 1950, Braun-Blanquet 1961, Schwabe & Kratochwil 2004). These valleys display xerothermic vegetation complexes, in which various types of dry grasslands are a major element (Dengler 2018). The upper Rhone valley in the Swiss canton of Valais is one of the deepest and thus driest and most continental of these valleys (Braun-Blanquet 1961). Here the xerothermic flora is particularly rich, comprising many different elements such as steppic species with their isolated westernmost range outposts, sub-Mediterranean species, dealpine and widespread European dry grassland species, enriched with some regional endemics (for some examples, see Dengler et al. 2019). Actually, the Valais was so famous among botanists that many dry grassland species were named after it, including *Festuca valesiaca* (main distribution range in the steppe biome of Eurasia), *Koeleria vallesiana* (main distribution in sub-Mediterranean Iberia) and *Centaurea valesiaca* (endemic of Valais and other dry valleys of the Western Alps).

Some of the classical syntaxonomic works were from the Valais (Frey 1934, Braun-Blanquet & Richard 1950) or the inner-alpine dry valleys in general (Braun-Blanquet 1961), but in the subsequent decades, only few regional phytosociological studies have been conducted in Switzerland. There are two overviews of the higher vegetation types of Switzerland from recent decades (Theurillat et al. 1995, Delarze et al. 2015), but Switzerland, unlike many other European countries (e.g. Berg et al. 2004, Chytrý 2007, Janišová 2007), has not yet seen broad-scale syntaxonomic revisions based on consistent analyses of large amounts of vegetation plots. Newer syntaxonomic concepts of the class *Festuco-Brometea*, which found strong support over huge areas of Central and Eastern Europe (e.g. Willner et al. 2017, 2019), have thus not been tested in Switzerland so far. During a student course in Ausserberg, Valais, the first author of this article got the impression that those concepts might actually better reflect the floristic and ecological relationships of the dry grasslands in the region than the Swiss “standard typology” by Delarze et al. (2015). This prompted sampling of plots during three occasions to subject these impressions to the scrutiny of numerical analyses.

Specifically, we asked: (1) Which main types of dry grasslands occur in Ausserberg, and how are they dis-

tinguished floristically and ecologically? (2) How could these types be best reflected in a European syntaxonomic scheme, and how does this relate to the Swiss concept? (3) How are species richness patterns of these communities at different spatial scales and their species-area relationships related to those of *Festuco-Brometea* communities elsewhere?

Methods

Study area

The study was conducted on the south-facing slopes of the Rhone valley in the canton of Valais, Switzerland, above the village Ausserberg (Figure 1). The upper Rhone valley is one of the inner-alpine dry valleys characterised by the occurrence of isolated steppic vegetation (Christ 1879, Braun-Blanquet 1961). A mean annual precipitation of only 596 mm in Visp on the valley floor at 639 m a.s.l. (MeteoSchweiz 2016) in approximately 1.5 km distance from the study area underlines the very dry conditions. The study area comprises elevations from 1050 to 1320 m a.s.l. and a surface of approx. 1 km². The underground is a mosaic of metamorphic granite and gneiss, dolomite and glacial moraine debris from the last ice age (Marthaler et al. 2017).

Far into the 20th century, the region was dominated by subsistence agriculture. Irrigation by traditional water channels was mainly used for hay meadows and vineyards. The non-irrigated areas above the uppermost water channel were cultivated with small-scale rye fields, whereas rocky areas with shallow soils were grazed (Christ 1879, Crook & Jones 1999). Nowadays traditional irrigation systems are largely replaced by modern devices such as aerial sprinkler systems, often in combination with fertilisation to increase yields (e.g. Boch et al. 2018a). While irrigated grasslands are still mown or grazed, former arable areas have been transformed to extensive pastures, and less productive land has been abandoned. Consequently, the actual vegetation is a diverse mosaic of small-scale pastures and meadows ranging from mesic to dry, successional forests, scrubs, *Juniperus sabina* heath, forest edge communities and steppic vegetation.

Field sampling

In 2018 we sampled a total of 28 10-m² vegetation plots in different types of dry grasslands above the village of Ausserberg (Figure 1). They were selected to be internally homogenous, but to represent the variability of dry grasslands in the area studied. The first 12 plots (plot IDs VSR001–VSR012) were recorded in June by a

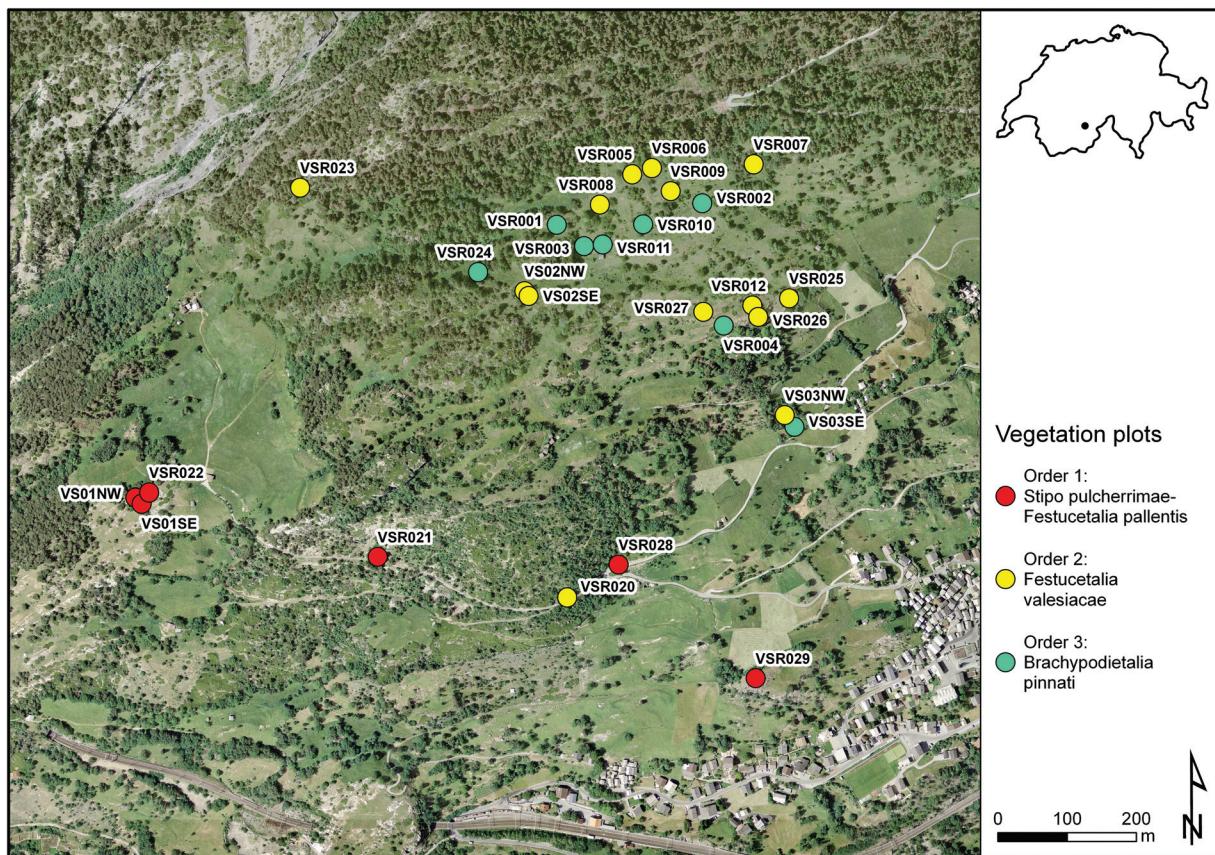


Figure 1: Map of the study area and its location within Switzerland. The village of Ausserberg is in the southeast corner. The 28 plots are labelled with their ID. Copyright geodata: swisstopo DV084370.

Slika 1: Zemljevid obravnavanega območja in njegova lokacija v Švici. Vas Ausserberg je v jugovzhodnem kotu. 28 popisnih ploskev je označenih z njihovo oznako ID. Avtorske pravice geodata: swisstopo DV084370.

Bachelor student class supervised by J.D. using circular plots according to the standard of the Swiss national biodiversity monitoring programmes (Koordinationsstelle BDM 2014, Boch et al. 2018b). In these plots only vascular plants and some simple environmental and structural parameters were recorded. The remaining 16 plots were sampled in September during an excursion of J.D. and I.D. (VSR020–VSR027) and during a “retreat” of the Research Group Vegetation Ecology of the ZHAW (VSR028–VSR029, VS01–VS03). These 16 plots were square-shaped; in addition to vascular plants, also tericolous bryophyte and lichen species were sampled, and mixed soil samples of the uppermost 10 cm were taken. Furthermore, three nested-plot series of 0.0001 to 100 m² grain sizes were sampled according to the EDGG standard (Dengler et al. 2016) during the “retreat”.

In the 10-m² plots, all species were noted and their percentage coverage estimated with the shoot presence method. In addition, the cover of the individual vegetation layers and of litter were estimated. The height of the

herb layer was measured at its maximum as well as with the disc method in five points (Dengler et al. 2016) and expressed as average and standard deviation. Likewise, the fractional cover of fine soil, gravel, stones and rocks at the soil surface were estimated. We further determined slope inclination and aspect as well as maximum microrelief (Dengler et al. 2016). Inclination and aspect were used to calculate the heat load index according to Olsson et al. (2009). Soil depth was measured in five points with a pointed iron pole of 85 cm length and expressed as mean and standard deviation (Dengler et al. 2016).

Nomenclature of vascular plants follows Juillerat et al. (2017) except for *Hieracium velutinum* Hegetschw., which we accepted as separate species from *H. pilosella* due to its morphological, ecological and chorological distinctness, that of bryophytes Meier et al. (2013) and that of lichens Nimis et al. (2018). The recorded plots are stored in and are available from the GrassPlot database (Dengler et al. 2018b). They are also part of an emerging Swiss National Vegetation Database (“Veg.CH”).

Soil analyses

The soil samples were dried for two days at 40 °C and sieved to < 2 mm. Soil skeleton proportion was determined by weighing the samples before and after sieving. The soil pH and conductivity were determined with a multimeter HQ11d (Hach Lange GmbH) using an IntelliCAL PHC101 (SN172262567043) electrode to measure the soil pH and an CDC401 (SN103262581003) electrode for conductivity in the supernatant of a soil suspension using a 1:2.5 mixture of soil and 0.01 M CaCl₂ (for pH) and distilled water (for conductivity), respectively (ART/ACW 2008). For measuring the content of organic and inorganic carbon as well as nitrogen, the samples were ground for 36–90 s with a pebble mill MM400 (Retsch). From each sample two subsamples of 100–110 mg were put into tin boats and analysed using a TruSpec Macro Analyser (by Leco, SN3378) by burning them at 550 °C for C_{org} and 950 °C for C_{tot}.

Statistical analyses

We subjected the vegetation data to modified TWINS-PAN (Roleček et al. 2009) using JUICE (Tichý 2002) and checked how well the outcomes of different resolutions were characterised floristically and whether they could be interpreted ecologically. For this purpose, species that were identified with uncertainty or only to the genus level as well as bryophytes and lichens were excluded. For the selected classification, we then determined diagnostic species with the phi-coefficient of association standardised for groups of equal plot number (Tichý & Chytrý 2006). For this procedure, bryophytes and lichens were included, but their constancies were calculated only for the subset of plots in which they had been recorded. We accepted species with phi > 0.6 as highly diagnostic and those with phi > 0.3 as diagnostic, provided the concentration was significant according to Fisher's exact test at $\alpha = 0.05$.

We calculated mean cover-weighted ecological indicator values ranging from 1 to 5 according to Landolt et al. (2010) using the R software environment (R Core Team 2018) and the function "functcomp" of the "FD" package (Laliberté et al. 2014). The mean indicator values, the species richness and structural data as well as the soil and other metric environmental data were then subjected to an analysis of variance (ANOVA), followed by Tukey's post hoc test (function "HSD.test" of the "agricolae" package by de Mendiburu (2019)) in case of significant results to test for differences between the distinguished vegetation units. We used the program Canoco (Ter Braak & Šmilauer 2012) to perform Detrended

Correspondence Analysis (DCA), in which environmental parameters with significant differences between vegetation units were displayed as supplementary variables. Species-area relationships of the three nested-plot series were approximated by power functions by applying linear regression to the log₁₀-transformed values of area in m² (*A*) and species richness (*S*) (Dengler 2009):

$$\log_{10} S = \log_{10} c + z \log_{10} A$$

Assignment to the Swiss classification scheme

In Switzerland, the only existing "phytosociological classification scheme" is that of Delarze et al. (2015). While aiming at being a comprehensive habitat classification of the country, the distinguished habitat types mainly correspond to phytosociological alliances (sometimes also suballiances or groups of alliances), and they are described in phytosociological terms. The habitat typology of Delarze et al. (2015) also underlies the national Red List of Habitats (Delarze et al. 2016) and is thus central in many conservation assessments. For the lower ranks of the habitat typology, the book proposes a bottom-up approach to identify the habitat type by relating a vegetation relevé to possible habitat types in a cross table. The table is filled in with different symbols for the different diagnostic values of species, which finally helps to choose the most probable habitat type. As the book does not contain numerical weights for the four different types of diagnostic species, we adopted the implementation of the approach proposed by its co-author S. Eggenberg (pers. comm.): dominant character species present with $\geq 5\% - 6$ points; dominant character species present with $< 5\% - 4$ points; character species present – 4 points; dominant typical species present with $\geq 5\% - 2$ points; dominant typical species present with $< 5\% - 1$ point; typical species present – 1 point. In essence, this provides a manual or electronic expert system, which enables the automatic and unambiguous assignment of relevés to the units of Delarze et al. (2015) ("supervised classification"). We implemented this in MS Excel for the nine ecologically and floristically most probable habitat/vegetation types. For each of our plots, we thus got scores for the match with each of the nine types. We selected the type with the highest score and mention the second highest if there was only a small difference.

Results

Flora

We found a total of 217 taxa (excluding uncertainly identified taxa), comprising 196 vascular plant, 14 bryophyte and 7 lichen taxa. Though most of the sampling took place rather late in the year, we could still record numerous annual vascular plants in the plots (e.g. *Alyssum alyssoides*, *Arenaria serpyllifolia*, *Lithospermum arvense*, *Veronica dilenii*, *V. praecox*, *V. verna*), indicating that our vascular plant species lists should be rather complete. However, we might have missed some ephemeral mosses and liverworts that show only from autumn to spring.

Biodiversity

Mean richness of all species increased from 1.7 on 1 cm² to 47.3 on 100 m² (Table 1). Bryophytes and lichens contributed little to the overall biodiversity with an average of only 4.3 species (9.1%) on 100 m². For areas from 100 or 1000 cm² onwards, the species-area relationship for total richness very closely followed a power function, whereas at very fine grain sizes, it showed a positive deviation, i.e. no further decrease in richness with decreasing area. Merging all three nested-plot series and all grain sizes, a power law described the SAR reasonably well ($R^2 = 0.967$ for linear regression in double-log space): *Total species richness = 13.4 (Area / m²)^{0.27}*.

Vegetation classification

At the first level, modified TWINSPAN separated the rocky grasslands (“Order 1”) from the rest (“Order 2” and “Order 3” in Table 2), but the latter was floristically

not well characterised. Allowing three clusters, all were very well characterised floristically and ecologically and could easily be identified with described phytosociological units (see Discussion), whereas the pattern became blurred again at higher cluster resolutions. Therefore, we adopted the three-cluster solution (Table 2) without further modification, though one could argue that some relevés might be transitional between the clusters or towards other units (see Table 3).

Characterisation of the three clusters

Cluster 1 mainly represents rocky dry grasslands, cluster 2 non-rocky dry grasslands and cluster 3 non-rocky semi-dry grasslands. The clusters differed significantly in many of the analysed biodiversity, structural and ecological variables (Table 4). Stands of clusters 2 and 3 had a nearly twice as high herb layer cover than those of cluster 1. Moreover, cluster 1 was distinguished from the two other clusters by much higher inclination and heat load index, more gravel on the surface and lower humus content (C_{org}). By contrast, for several of the mean indicator values, the two xeric clusters 1 and 2 were opposed to the meso-xeric cluster 3, namely by lower moisture, lower nutrients, lower humus and higher continentality. Finally, for some of the parameters, there was a sequence from cluster 1 (xeric, rocky) via cluster 2 (xeric, non-rocky) to cluster 3 (meso-xeric), namely a decrease in pH, an increase in nitrogen and changes in mean indicator values that indicate decreasing aeration of the soil, decreasing light availability, but increasing mowing tolerance. This overall pattern is well reflected in the ordination diagram, in which the three clusters are well separated (Figure 2). The spatial distribution of the plots (Figure 1) suggests

Table 1: Mean, minimum and maximum species richness in our plots. *: non-vascular plants were recorded only in 16 of the 28 plots so that richness of all species, bryophytes and lichens is available only for these.

Tabela 1: Povprečno, najmanjše in največje število vrst na ploskvah. *: nižje rastline smo beležili le na 16. od 28 ploskev in je pestrost vseh vrst, mahov in lišajev, na voljo le za te.

Area [m ²]	n	All species			Vascular plants			Bryophytes	Lichens
		Mean	Min.	Max.	Mean	Min.	Max.		
0.0001	6	1.7	1	3	1.7	1	3	0.0	0.0
0.001	6	1.7	1	3	1.7	1	3	0.0	0.0
0.01	6	2.7	2	4	2.7	2	4	0.0	0.0
0.1	6	7.0	4	11	7.0	4	11	0.0	0.0
1	6	14.7	10	23	14.7	10	23	0.0	0.0
10	16 or 28*	28.1	18	40	26.8	15	47	1.7	0.6
100	3	47.3	37	54	43.0	33	54	2.3	1.3

Table 3: Comparison of our classification with the most likely habitat type determined with Delarze et al. (2015). Orders are those of our adopted syntaxonomic scheme: O1 = *Stipo pulcherrimae-Festucetalia pallentis*, O2 = *Festucetalia valesiacae*, O3 = *Brachypodietalia pinnati*. Transitional plots were determined based on expert knowledge using the order typology of Mucina et al. (2016). Delarze ID and Delarze alliance refer to the habitat that got the highest score when applying the assignment rules of S. Eggenberg (pers. comm.) to the lists of diagnostic species in Delarze et al. (2015). Correct = + means a direct match, correct = (+) means that the habitat type determined with Delarze et al. (2015) corresponds at least to our second option when we considered a certain relevé transitional. The *Stipo-Poion* of Delarze et al. (2015) was counted as matching with both O1 and O2.

Tabela 3: Primerjava naše klasifikacije z najbolj podobnim habitatnim tipom, določenim v skladu z Delarze et al. (2015). Redovi so v skladu z našo sintaksonomsko shemo: O1 = *Stipo pulcherrimae-Festucetalia pallentis*, O2 = *Festucetalia valesiacae*, O3 = *Brachypodietalia pinnati*. Prehodne ploskve smo uvrstili na osnovi ekspertnega znanja s tipologijo po Mucina et al. (2016). Oznake Delarze ID in Delarze alliance se nanašajo na habitat, ki je dobil najvišjo vrednost pri uporabi pravil uvrščanja po S. Eggenbergu (osebno sporočilo) in po seznamu diagnostičnih vrst po Delarze et al. (2015). Correct = + pomeni neposredno ujemanje, correct = (+) pomeni, da habitatni tip, določen po Delarze et al. (2015) odgovarja vsaj drugi možnosti, če smo popis označili kot prehoden. Zvezo *Stipo-Poion* po Delarze et al. (2015) smo upoštevali, kot da se ujema z obema redovoma O1 in O2.

Plot ID	Order	Transitional to order	Delarze ID	Delarze alliance	Correct
VS01NW	O1		4.2.1.1	<i>Stipo-Poion</i>	+
VS01SE	O1		4.2.1.1	<i>Stipo-Poion</i>	+
VSR021	O1		4.1.1	<i>Alyso-Sedion</i>	
VSR022	O1		4.2.1.1 / 4.1.1	<i>Stipo-Poion / Alyso-Sedion</i>	+
VSR028	O1	<i>Sedo-Scleranthesetalia</i>	4.2.1.1	<i>Stipo-Poion</i>	+
VSR029	O1	O2	4.2.1.1	<i>Stipo-Poion</i>	+
VS02NW	O2		4.2.1.1	<i>Stipo-Poion</i>	+
VS02SE	O2		4.2.1.1	<i>Stipo-Poion</i>	+
VS03NW	O2		4.2.1.1	<i>Stipo-Poion</i>	+
VSR005	O2	<i>Sedo-Scleranthesetalia</i>	4.1.3	<i>Sedo-Veronicion</i>	(+)
VSR006	O2		4.1.3	<i>Sedo-Veronicion</i>	
VSR007	O2		4.1.3	<i>Sedo-Veronicion</i>	
VSR008	O2		4.2.1.1	<i>Stipo-Poion</i>	+
VSR009	O2	O3 or <i>Antherico-Geranieta</i>	5.1.1	<i>Geranion sanguinei</i>	(+)
VSR012	O2		5.1.1	<i>Geranion sanguinei</i>	
VSR020	O2	O1 or <i>Antherico-Geranieta</i>	4.2.1.1 / 5.1.1	<i>Stipo-Poion / Geranion sanguinei</i>	+
VSR023	O2	O1	4.2.1.2	<i>Cirsio-Brachypodium</i>	
VSR025	O2		4.2.1.1 / 4.6.1	<i>Stipo-Poion / Convolvulo-Agropyron</i>	+
VSR026	O2		4.2.1.1	<i>Stipo-Poion</i>	+
VSR027	O2		4.2.1.1	<i>Stipo-Poion</i>	+
VS03SE	O3		4.2.4 / 4.5.1	<i>Mesobromion / Arrhenatherion</i>	
VSR001	O3	<i>Agropyretalia intermedio-repentis</i>	4.6.1	<i>Convolvulo-Agropyron</i>	(+)
VSR002	O3		4.6.1	<i>Convolvulo-Agropyron</i>	
VSR003	O3		5.1.1	<i>Geranion sanguinei</i>	
VSR004	O3		5.1.1	<i>Geranion sanguinei</i>	
VSR010	O3	<i>Antherico-Geranieta</i>	4.6.1	<i>Convolvulo-Agropyron</i>	
VSR011	O3		4.5.1	<i>Arrhenatherion</i>	
VSR024	O3		4.2.1.2	<i>Cirsio-Brachypodium</i>	+

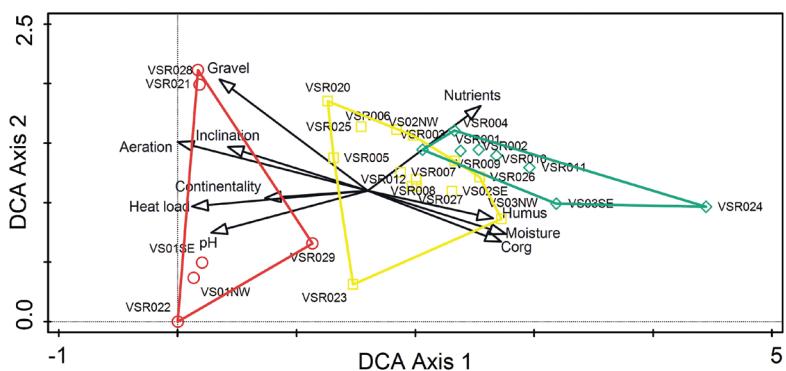
Table 4: Mean species richness and structural and environmental parameters in the plots of the three distinguished orders. The p -values are from the ANOVAs. The superscript letters indicate homogeneous groups according to Tukey's posthoc test at $\alpha = 0.05$.

Tabela 4: Povprečna vrstna pestrost in strukturni ter okoljski parametri na ploskvah, razdeljenih na tri redove. p-vrednosti so dobljene z analizo ANOVA. Nadpisane črke označujejo homogene skupine v skladu s Tukeyevim posthoc testom pri $\alpha = 0.05$.

	Order 1	Order 2	Order 3	p		Order 1	Order 2	Order 3	p
Species richness on 10 m²									
All species	30.2	24.8	35.0	0.938	All species	30.2	24.8	35.0	0.938
Vascular plants	26.3	24.3	31.6	0.103	Vascular plants	26.3	24.3	31.6	0.103
Bryophytes	2.8	1.5	1.0	0.089	Bryophytes	2.8	1.5	1.0	0.089
Lichens	1.0	0.4	0.0	0.047	Lichens	1.0	0.4	0.0	0.047
Vegetation structure									
Mean vegetation height (cm)	6.7	9.3	5.6	0.807	SD soil depth (cm)	6.4	6.7	8.7	0.419
SD vegetation height (cm)	5.5	7.7	2.9	0.873	Skeletal content (%)	24	19	24	0.705
Maximum vegetation height (cm)	80	90	109	0.100	pH [CaCl ₂]	6.62 ^a	5.81 ^{ab}	5.30 ^b	0.008
Vegetation total (%)	41 ^b	75 ^a	76 ^a	0.001	Electrical conductivity ($\mu\text{S cm}^{-1}$)	192	162	125	0.066
Shrub layer (%)	0.0 ^a	0.3 ^a	8.4 ^a	0.036	C _{org} (%)	4.0 ^b	6.3 ^a	8.2 ^a	0.002
Herb layer (%)	40 ^b	74 ^a	72 ^a	0.003	C _{inorg} (%)	0.7	0.6	0.8	0.958
Moss layer (%)	1.5	0.6	3.6	0.304	N (%)	0.4 ^b	0.5 ^{ab}	0.6 ^a	0.001
Topography									
Inclination (°)	37 ^a	22 ^b	20 ^b	0.007	C/N	11.1	12.9	13.2	0.152
Heat load index	0.51 ^a	0.05 ^b	0.05 ^b	0.005	Ecological indicator values				
Maximum microrelief (cm)	12.7	7.4	19.3	0.275	Moisture (F)	1.4 ^b	1.4 ^b	2.1 ^a	<0.001
Soil surface									
Litter (%)	32	32	37	0.998	Reaction (R)	3.9	3.8	3.7	0.275
Stones (%)	37 ^a	37 ^a	9 ^a	0.043	Nutrients (N)	2.1 ^b	2.2 ^b	2.5 ^a	<0.001
Gravel (%)	9 ^a	3 ^b	0 ^b	0.006	Humus (H)	2.0 ^b	2.1 ^b	2.7 ^a	0.003
Fine soil (%)	48	87	77	0.145	Aeration (D)	4.0 ^a	3.3 ^b	2.8 ^c	<0.001
Soil parameters									
Mean soil depth (cm)	8.6	13.4	16.7	0.128	Light (L)	4.1 ^a	3.9 ^b	3.8 ^c	<0.001
					Temperature (T)	3.8	4.0	3.7	0.139
					Continentiality (K)	4.3 ^a	4.3 ^a	3.8 ^b	0.002
					Mowing tolerance (MV)	1.8 ^c	2.1 ^b	2.6 ^a	<0.001
					Influence of man on site conditions (EM)	2.3	2.2	2.4	0.326

Figure 2: DCA of the dry grassland samples of Ausserberg. Axis 1 explains 17.2% of the variation, Axis 2 explains 8.1%. Red = Order 1: *Stipo pulcherrimae-Festucetalia pallentis*, yellow = Order 2: *Festucetalia valesiacae*, green = Order 3: *Brachypodietalia pinnati*.

Slika 2: DCA popisov suhih travnišč pri vasi Ausserberg. Os 1 pojasnjuje 17,2% variacije, os 2 pa 8,1%. Rdeča = red 1: *Stipo pulcherrimae-Festucetalia pallentis*, rumena = red 2: *Festucetalia valesiacae*, zelena = red 3: *Brachypodietalia pinnati*.



that cluster 1 largely comprises currently unused, largely natural stands, whereas stands of clusters 2 and 3 are currently mostly extensively grazed or mown; many of them have developed on ex-arable fields that were abandoned some decades ago.

Floristically, the three clusters are united by the frequent occurrence of several widespread *Festuco-Brometea* species such as *Phleum phleoides*, *Bromus erectus*, *Helianthemum nummularium*, *Teucrium chamaedrys* and *Stachys recta* (see Companion species in Table 2). Cluster 1 is mainly sepa-

rated by a group of extremely drought-tolerant tussock grasses (*Koeleria vallesiana*, *Stipa eriocaulis*, *Festuca pallens*, *Melica ciliata*), succulents (*Sedum album*, *Sempervivum tectorum*), annual herbs (e.g. *Acinos arvensis*, *Alyssum alyssoides*) and various non-vascular species (e.g. *Bryum argenteum*, *Encalypta vulgaris*, *Placidium squamulosum*). Moreover, several herbs that are frequent in clusters 2 and 3 are nearly absent (*Carex caryophyllea*, *Potentilla argentea*, *Vicia angustifolia*). Cluster 2 is physiognomically characterised by a high cover of *Festuca valesiaca*, which is also diagnostic. Moreover, some perennial forbs (e.g. *Dianthus carthusianorum*, *Peucedanum oreoselinum* and *Pulsatilla montana*) as well as some ephemeral species (*Veronica verna*, *Poa bulbosa*, *Arabis nova*) are concentrated here. Cluster 3, finally, in most cases has a high cover of *Bromus erectus*, but often also a relatively high cover of *Festuca valesiaca*. It is differentiated by a few typical *Festuco-Brometea* species (*Poa angustifolia*, *Galium verum*, *Sanguisorba minor*), a forest-edge species (*Trifolium alpestre*), several species that have their main occurrence in mesic grasslands (e.g. *Lathyrus pratensis*, *Taraxacum officinale* aggr., *Veronica chamaedrys*) and some tree encroachment (e.g. *Fraxinus excelsior*). Some typical species of meso-xeric basiphilous grasslands occur in certain plots, but were too rare in Ausserberg to qualify them as diagnostic species locally (e.g. *Hieracium pilosella*, *Ranunculus bulbosus*, *Trifolium montanum*, *Brachypodium rupestre*, *Pimpinella saxifraga* aggr.).

Assignment to the Swiss classification scheme

Overall, we found a match of 50%, or a bit more if transitional stands are also counted, between our assignment and that using the supervised Swiss classification (Table 3). While our clusters 1 and 2 were in the majority of cases correctly assigned to the *Stipo-Poion* in the sense of Delarze et al. (2015), some were placed in the *Alyssonion* or *Sedo-Veronicion*. Generally, the discrepancy between our classification and the expert system based on Delarze et al. (2015) was much bigger for the meso-xeric cluster 3. Only one of our eight relevés was identified as *Cirsio-Brachypodion* by the expert system, whereas other assignments prevailed: *Convolvulo-Agropyrrion*, *Geranion sanguinei*, *Arrhenatherion* and *Mesobromion*.

Discussion

Peculiarities of the flora

During our vegetation sampling, we found many interesting species (Table 2). Five of them are subsequently discussed as only few localities were previously known

from Switzerland or because of their supraregional peculiarity.

Festuca pallens from the *F. ovina* aggregate occurred in six of our 28 plots and was diagnostic for the first cluster, which is in agreement with broad-scale analyses in Europe (Schaminée et al. 2016, Willner et al. 2017, 2019), which recognise it as one of the best diagnostic species of the order *Stipo pulcherrimae-Festucetalia pallentis*. The knowledge on distribution (see <https://www.infoflora.ch/en/flora/festuca-pallens.html>) and sociological behaviour of this species in Switzerland is still fragmentary as until recently it has not or not correctly been distinguished from other species of the *Festuca ovina* aggregate. Nowadays it is considered “near threatened” (Bornand et al. 2016).

Astragalus exscapus is a rare and threatened steppe relict species with several disconnected distribution ranges in eastern Central and Eastern Europe (Becker 2013). In the inner-alpine valleys of Valais and Aosta, it has its westernmost isolated occurrences (Becker 2013), and it is considered “near threatened” in Switzerland (Bornand et al. 2016). In historic excursion reports from the research area, the species was mentioned to occur at “every step and turn” (e.g. Frey-Huber 1952). We also occasionally found it beside the paths, but it occurred in only one of our 10-m² plots, VSR023, dominated by *Carex humilis*.

Hieracium velutinum Hegetschw. (*Pilosella velutina* (Hegetschw.) F.W. Schultz & Sch. Bip.) has not been distinguished from *H. pilosella* (*P. officinarum*) at species or subspecies rank in Swiss floras up to now (e.g. Eggenberg et al. 2018), whereas in Italy (Pignatti 2018) and Austria (Fischer et al. 2005), it is accepted as a species and in the Euro+Med PlantBase as a subspecies (Euro+Med 2006–2019). The taxon is very distinct from *H. pilosella* due to its nearly white upper leaf surface caused by a dense cover of stellate hairs. *H. velutinum* is ecologically and chorologically quite different from “normal” *H. pilosella* as it appears to be restricted to very dry sites in the continental valleys of the Alps (Austria, Switzerland, Italy and France), but there ranging from 500 to 2800 m a.s.l. (Fischer et al. 2005, Pignatti 2018), with occurrences also on the Iberian Peninsula (Euro+Med 2006–2019). In Ausserberg it can be found regularly in very dry places, including our plot VSR020. The first author knows this species also from various places in Zermatt (Valais), Pontresina (Engadine) and Cogne (Aosta valley, Italy). It appears worthwhile to consider it a distinct taxon in future studies.

Ceratodon conicus is an acrocarpous moss species, of which only very few recent records exist from Switzerland, approximately half of them from the Valais (Roloff & Urmi 2019). According to Schnyder et al. (2004), the species is threatened in Switzerland. However, it seems likely that the species has frequently been overlooked due

to its similarity to the common *Ceratodon purpureus*. We found the species in three out of 16 plots in which bryophytes were sampled. This supports the assumption of Amann (1933) that the species is likely to be more common in Switzerland than hitherto assumed, especially in the warmer regions of the country.

Cladonia novochlorophaea, a lichen species with a primary thallus of small squamules and usually dark brown cup-like podetia, belongs to the *C. grayi* group. It can only be identified correctly by chemical analysis of secondary compounds using thin-layer chromatography (TLC). Before, it was mentioned to grow on acidic soil over siliceous rocks and in arctic-alpine heaths. While it is regarded as widespread but not common, only a few records in the Alps are known so far (Nimis et al. 2018) and only one from Switzerland in the canton of Luzern (see <http://www.swisslichens.ch>). We found this species in two of our 10-m² plots.

Biodiversity

Compared to *Festuco-Brometea* communities in general, those of Ausserberg were less diverse across all scales. Dengler et al. (2018a) reported mean vascular plant richness values for stands of this class in Europe of 8.0 on 0.01 m², 21.0 on 1 m², 34.9 on 10 m² and 54.1 on 100 m², compared to only 2.7, 14.7, 26.8 and 43.0 species in Ausserberg. The values are far below grassland diversity hotspots like Transylvania in Romania or the White Carpathians in the Czech Republic (Dengler et al. 2012, Wilson et al. 2012). However, they are very similar to those found in *Festuco-Brometea* communities of the Aosta valley, another inner-alpine dry valley of the Western Alps (Wiesner et al. 2015), where the average vascular plant species richness on 10 m² was 27.8. This finding might indicate that dry grasslands of the most extreme (continental) climates are less diverse than those of dry sites in more benign climates. While in Ausserberg the richness differences between the three orders were not significant for “all taxa” and “vascular plants” (Table 4), their richness ranking corresponds to the generally acknowledged pattern that semi-dry grasslands are much richer than either of the two xeric orders (e.g. Dengler et al. 2012; Wiesner et al. 2015).

Syntaxonomy

The adopted three-cluster resolution could easily be identified with the three orders of the class *Festuco-Brometea* repeatedly found in broad-scale numerical analyses of the class in extra-alpine Central and Eastern Europe (e.g. Dengler et al. 2012, Willner et al. 2017, 2019). The rocky dry grasslands of order 1 correspond to the *Stipo*

pulcherrimae-Festucetalia pallentis, the xeric, non-rocky grasslands of order 2 to the *Festucetalia valesiacae* and the meso-xeric grasslands of order 3 to the *Brachypodietalia pinnati*. This tripartition of orders was also adopted in the first European Red List of Habitats (Janssen et al. 2016) and the re-definition of EUNIS habitat types using an electronic expert system (Schaminée et al. 2016). In these two European sources, the three orders are referred to as “E1.1g – Perennial rocky grassland of Central Europe and the Carpathians” (*Stipo pulcherrimae-Festucetalia pallentis*), “E1.2b – Continental dry steppe” (*Festucetalia valesiacae*) and “E1.2a – Semi-dry perennial calcareous grassland” (*Brachypodietalia pinnati*), respectively.

Until recently, following the tradition of Braun-Blanquet (1961), the xeric *Festuco-Brometea* communities of Valais, whether rocky or not, were united in a single alliance *Stipo-Poion xerophilae* placed in the *Festucetalia valesiacae* (Theurillat et al. 1995, Delarze et al. 2015, Mucina et al. 2016). Braun-Blanquet (1961) had used this alliance name only for the communities of the Eastern Alps (Engadine eastwards) and distinguished a separate alliance *Stipo-Poion carniolicae* (*recte: Stipo-Poion concinnae*) for the Western Alps, such as the Valais. Theurillat et al. (1995) united both of them as suballiances in the *Stipo-Poion xerophilae*, an approach recently followed by Mucina et al. (2016). We now can confirm that the *Stipo pulcherrimae-Festucetalia pallentis* also occurs in the Swiss inner-alpine valleys, as could have been inferred from the occurrence of many typical species (e.g. *Stipa eriocaulis*, *Festuca pallens*, *Carex humilis*) next to typical *Festucetalia valesiacae* communities. That the separation of the three orders is also valid and meaningful in Switzerland, can be seen in the TWINSPAN analysis (Table 2), where they appeared without any further manual modification, and in the ordination, in which the three orders are well separated (Figure 2). Further, on the first level of division of TWINSPAN, the *Festucetalia valesiacae* were still joined with the *Brachypodietalia pinnati* and opposed to the *Stipo pulcherrimae-Festucetalia pallentis*. Likewise, *Festucetalia valesiacae* and *Stipo pulcherrimae-Festucetalia pallentis* differed in many structural and environmental parameters (Table 4).

The fact that in Switzerland both orders have traditionally been merged creates some nomenclatural confusion. The non-rocky stands are very similar to the *Festucion valesiacae* in eastern Central Europe (e.g. Czech Republic: Chytrý 2007, Hungary: pers. observations J.D.). Therefore, there is no reason for a separate alliance. Likewise, Wolfgang Willner (Vienna, pers. comm.) considers the type of the eastern alpine *Stipo-Poion xerophilae* to belong to the *Festucion valesiacae*, whereby the *Stipo-Poion xerophilae* becomes a later syntaxonomic synonym of the *Festucion valesiacae*. By contrast, the rocky dry grasslands

of Valais are floristically so distinct from the *Stipo pulcherrimae-Festucetalia pallentis* alliances described elsewhere (e.g. Austria, Czech Republic or Germany: Mucina & Kolbek 1993, Chytrý 2007, pers. observation J.D.) that a separate alliance appears justified. The question thus was whether the name *Stipo-Poion concinnae* would be applicable to this. The holotype of this alliance is the *Koelerio vallesianae-Poetum concinnae* (Braun-Blanquet & Richard 1950, Terzi et al. 2016). While among the eight relevés in the original description (Braun-Blanquet & Richard 1950) some can be seen as transitional to the *Festucion valesiacae*, we chose a type relevé that allows using this alliance name for the rocky dry grasslands of the inner-alpine dry valleys:

Koelerio vallesianae-Poetum concinnae Br.-Br. & Richard 1950: Braun-Blanquet & Richard (1950: Table 2: Relevé No. 8) *lectotypus hoc loco*

Proposed syntaxonomic scheme

We use here the names accepted in the EuroVegChecklist (Mucina et al. 2016), except for the *Stipo-Poion concinnae*, which in the EuroVegChecklist is considered a syntaxonomic synonym of the *Stipo-Poion xerophilae* Br.-Bl. & Richard 1950. In brackets we additionally provide the names suggested by Terzi et al. (2017) if they are different.

Class: *Festuco-Brometea* Br.-Bl. & Tx. ex Soó 1947 (*Festuco-Brometea erecti* Br.-Bl. & Tx. ex Klika & Hadač 1944)

Order 1: *Stipo pulcherrimae-Festucetalia pallentis* Pop 1968 nom. conserv. propos.

Alliance: *Stipo-Poion concinnae* Br.-Bl. & Richard 1950

Order 2: *Festucetalia valesiacae* Soó 1947 (*Festucetalia valesiacae* Br.-Bl. & Tx. ex Br.-Bl. 1950 nom. conserv. propos.)

Alliance: *Festucion valesiacae* Klika 1931 nom. conserv. propos.

Order 3: *Brachypodietalia pinnati* Korneck 1974 nom. conserv. propos. (*Brometalia erecti* W. Koch 1926)

Alliance: *Cirsio-Brachypodion pinnati* Hadač & Klika in Klika & Hadač 1944

Relation to the Swiss habitat classification

Some relevés of the first two alliances were assigned to alliances of the class *Sedo-Scleranthetea* by the expert system based on Delarze et al. (2015). However, this ignores that it is just normal for *Festucetalia valesiacae* communities to contain a significant share of annuals and for *Stipo pulcherrimae-Festucetalia pallentis* communities to contain both

annuals and succulents (e.g. Schaminée et al. 2016, Willner et al. 2017, 2019). Only when perennial tussock grasses are largely absent on several square metres does it make sense to consider an assignment to the *Sedo-Scleranthetea*.

Regarding the very low “correct” assignment rates of the Delarze et al. (2015) expert system for the third order, it should be stressed that the majority of our relevés do not represent particularly typical *Cirsio-Brachypodion* stands and some of them have a slightly ruderal touch (more typical stands had been freshly mown or grazed at the time of recording so that we could not sample them; but see Figure 3c). However, the dominance of *Bromus erectus* and the presence of various *Festuco-Brometea* species as well as differential species from mesic sites leave little doubt that the relevés should be placed in the order *Brachypodietalia pinnati*, whereas the subdominance of *Festuca valesiaca* and the frequent presence of *Potentilla pusilla* clarify that the subcontinental *Cirsio-Brachypodion* rather than the *Mesobromion* is the appropriate alliance.

Conclusions and outlook

We could show that the “*Stipo-Poion*” of Swiss authors (but also Mucina et al. 2016) actually consists of two floristically and ecologically distinct units belonging to two widely accepted orders of the class *Festuco-Brometea*, the *Stipo pulcherrimae-Festucetalia pallentis* and the *Festucetalia valesiacae* (Mucina & Kolbek 1993, Dengler et al. 2012, Mucina et al. 2016, Willner et al. 2017, 2019). Given the widespread distribution of diagnostic species of both orders in the Valais, this is not surprising from a European perspective and was even predicted by the maps in Schaminée et al. (2016), but contrasts to the current syntaxonomic schemes of Switzerland (Delarze et al. 2015) and the Alps (Theurillat et al. 1995), where the order *Stipo pulcherrimae-Festucetalia pallentis* is not listed, not even as a synonym. These authors call the *Stipo-Poion* “*Innentalpine Felsensteppe*”, i.e. inner-alpine rocky steppe, a name that suggests that it should belong to the “rocky” order *Stipo pulcherrimae-Festucetalia pallentis*. However, they subordinate the *Stipo-Poion* to the order *Festucetalia valesiacae* typically growing on deep, non-rocky soils. Probably due to tradition and lack of recent synthetic vegetation studies from Switzerland, this concept was also followed by the EuroVegChecklist (Mucina et al. 2016).

While we were able to extend the known distribution range of the *Stipo pulcherrimae-Festucetalia pallentis* to the southwest, it remains unclear where inside the Alps the *Stipo-Poion concinnae* (as outlined here) occurs, for example, where it transgresses into the *Asplenio-Festucion pallentis* and the *Diantho lumnitzeri-Seslerion* of the Eastern



Figure 3: Typical examples of the three distinguished vegetation alliances, from top to bottom, (a) *Stipo-Poion concinnae*, order *Stipo pulcherrimae-Festucetalia pallentis* (on dolomite outcrops; with *Stipa eriocaulis* and *Carex humilis*), (b) *Festucion valesiacae*, order *Festucetalia valesiacae* (with *Festuca valesiaca*, *Dianthus carthusianorum* and *Linaria angustissima*) and (c) *Cirsio-Brachypodion pinnati*, order *Brachypodietalia pinnati* (with *Bromus erectus*, *Campanula glomerata*, *Centaurea scabiosa* and *Trifolium montanum*) (Photos: J. Dengler).

Slika 3: Značilni primeri treh zvez vegetacije od vrha navzdol: (a) *Stipo-Poion concinnae*, red *Stipo pulcherrimae-Festucetalia pallentis* (na dolomitu; z vrstama *Stipa eriocaulis* in *Carex humilis*), (b) *Festucion valesiacae*, red *Festucetalia valesiacae* (z vrstami *Festuca valesiaca*, *Dianthus carthusianorum* in *Linaria angustissima*) in (c) *Cirsio-Brachypodion pinnati*, red *Brachypodietalia pinnati* (z vrstami *Bromus erectus*, *Campanula glomerata*, *Centaurea scabiosa* in *Trifolium montanum*) (Fotografije: J. Dengler).

Alps (see Mucina & Kolk 1993, Mucina et al. 2016). Also the subdivision of the three now distinguished alliances of continental dry grasslands in Switzerland into associations and their distribution is largely unknown because the last and only broad-scale analysis of these vegetation types dates back to Braun-Blanquet (1961), whose concept of the class subdivision was quite different and whose associations and often also relevés were rather heterogeneous according to current standards so that an easy translation is not possible. An EDGG Field Workshop in the inner-alpine dry valleys of Switzerland in May 2019 will offer a first opportunity to reach a new broader-scale synthesis (Dengler et al. 2019). Further steps should then aim at data-driven classifications using the full range of relevés extant in Switzerland, determination of diagnostic species and ultimately the development of an electronic expert system (EES), which allows a plausible, reliable and unambiguous assignment of new Swiss relevés to syntaxa of any rank (for examples, see Janišová 2007, Schaminée et al. 2016, Willner et al. 2019).

Acknowledgements

We thank the participants of the field week of the Bachelor module “Lebensräume der Schweiz” in 2018, who sampled and digitised part of the vegetation data. We further thank Stefan Eggenberg for sharing his numerical weights for diagnostic values of species in Delarze et al. (2015) and Christine Keller for the identification of *Cladonia novochlorophaea* using TLC. We thank the handling editor (Orsolya Valkó) and three anonymous reviewers for the fast handling of the manuscript and constructive suggestions and Aiko Huckauf for linguistic editing.

Author contributions

J.D. conceived the idea of this study. Vegetation plots were recorded by a student field course supervised by J.D., during an excursion of I.D. and J.D. and during a two-day “retreat” of the Vegetation Ecology Group of the Institute of Natural Resource Sciences, ZHAW (J.D., M.B., R.B., J.G., D.H. and S.W.). A.B. determined critical bryophytes, S.B. the lichens, while J.G. analysed the soils. J.D. and E.S. classified the vegetation and determined the diagnostic species, S.R. calculated the numerical assignment to the Swiss habitat types, S.W. ran the other statistical analyses, and M.B. prepared the maps. J.D. led the writing with D.H. contributing the study area section and J.G. the soil analytical section. All authors revised the manuscript and approved the final version.

Jürgen Dengler , <https://orcid.org/0000-0003-3221-660X>
 Stefan Widmer , <https://orcid.org/0000-0002-4920-5205>
 Ariel Bergamini , <https://orcid.org/0000-0001-8816-1420>
 Steffen Boch , <https://orcid.org/0000-0003-2814-5343>
 Iwona Dembicz , <https://orcid.org/0000-0002-6162-1519>

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Table 2: Ordered vegetation table of the dry grasslands in Ausserberg, Valais, Switzerland. Significant diagnostic species with $\phi_i > 0.3$ are highlighted and presented in decreasing order (**: $\phi_i > 0.6$; *: $\phi_i > 0.3$). The values in the columns for individual relevés are cover values in %, the values in the constancy columns are constancies in %. Cover values $\geq 5\%$ are highlighted in bold.

Plot ID	Order 1						Order 2					
	VS01NW	VS01SE	VSR021	VSR022	VSR028	VSR029	VS02NW	VS02SE	VS03NW	VSR005	VSR006	VSR007
Non-vascular plants treated?	Y	Y	Y	Y	Y	Y	Y	Y	Y	N	N	N
Total vegetation cover [%]	50	45	30	27	45	51	80	80	80	95	95	75
Cover shrub layer [%]	0	0	0	0	0	0	0	0	0	0	3	0
Cover herb layer [%]	50	45	30	26	38	50	80	80	80	95	95	75
Cover moss layer [%]	0.1	0.01	0.1	1	7	1	0	0	0	0	0	0
Cover litter [%]	60	NA	7	20	25	50	90	80	60	95	10	NA
Cover stones and rocks [%]	30	NA	60	80	45	0.5	0	0	0.3	0	0	NA
Cover gravel [%]	5	NA	20	5	15	0	0	0	0	0	0	NA
Cover fine soil [%]	65	NA	20	15	40	99.5	100	100	99.7	100	100	NA
Species richness (total)	27	29	31	37	25	32	20	30	23	NA	NA	NA
Species richness (vascular plants)	24	26	29	29	22	28	20	26	23	25	15	22

Order 1: Stipo eriocalis-Festucetalia pallentis

B	Acinos arvensis	0.1	0.07	0.2	0.2	0.2
	Koeleria vallesiana	10	5	10	4	.	0.1
	Anthericum liliago	0.2	0.05	0.3	.	0.2	0.01
	Alyssum alyssoides	0.3	0.1	0.5	0.1
	Silene otites	0.1	0.05	.	0.3	.	0.5
B	Bryum argenteum	.	.	0.1	0.05	0.3	0.1
	Sedum album	1	0.5	0.3	1	1.5	.	.	.	1	.	.
	Stipa eriocalis	10	8	.	17	.	3
	Dianthus sylvestris	0.1	0.01	.	0.3
	Minuartia rubra	0.2	0.02	.	0.2
	Ononis pusilla	0.01	.	0.5	0.1
	Scabiosa triandra	.	0.05	.	0.5	.	0.1
	Festuca pallens	15	0.5	2	0.7
	Melica ciliata	0.5	.	2	0.5	0.5
	Sempervivum tectorum subsp. tectorum	1	1.5	.	12	12	0.1	.	.	3	.	2
L	Odontites luteus	.	0.01	.	0.1	0.5	0.01	.	0.01	.	.	.
	Thymus praecox subsp. praecox	0.5	0.02	.	1	0.3	.	.	.	0.5	.	.
	Caucalis platycarpos	.	.	0.1	.	1
	Centaurea valesiaca	.	0.05	.	.	.	0.1
	Encalypta vulgaris	.	0.1	.	0.025
L	Leptogium schraderi	0.1	0.1
L	Placidium squamulosum	0.2	.	.	0.2

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Tabela 2: Urejena vegetacijska tabela suhih travnišč pri vasi Ausserberg, Valais, Švica. Značilne diagnostične vrste z indeksom $f_i > 0,3$ so označene in urejene padajoče (**: $f_i > 0,6$; *: $f_i > 0,3$). Vrednosti v stolpcih za posamezne popise so pokrovnost v %, vrednosti v stolpcih stalnosti pa stalnost v %. Pokrovnost večja od $\geq 5\%$ je prikazana krepko.

VSR008 N	Order 2												Order 3												
	VSR009 N	VSR012 N	VSR020 Y	VSR023 Y	VSR025 Y	VSR026 Y	VSR027 Y	VSR03SE Y	VSR001 Y	VSR002 Y	VSR003 N	VSR004 N	VSR010 N	VSR011 N	VSR024 Y							All	O. 1	O. 2	O. 3
45	NA	NA	75	45	60	85	82	80	80	NA	85	75	60	70	85						41	75	76		
0	NA	NA	0.5	0	0	0	0	0	25	NA	30	4	0	0	0						0	0	0	8	
40	NA	NA	75	45	60	85	80	80	80	NA	80	70	55	70	70						40	74	72		
5	NA	NA	0.1	0.02	0	0.1	2	0	0	NA	0	0	0	15	10						2	1	4		
5	NA	NA	60	80	80	80	90	70	10	NA	85	10	25	12	50						32	66	37		
55	NA	NA	50	10	0	0	0	10	20	NA	0	15	0	20	0						43	10	9		
10	NA	NA	8	5	5	0	0	0	15	NA	0	0	60	20	0						9	3	14		
35	NA	NA	42	85	95	100	100	90	65	NA	100	85	40	60	100						48	87	77		
NA	NA	NA	30	27	18	28	22	40	NA	NA	NA	NA	NA	NA	30					30	25	35			
35	29	31	28	25	18	25	18	40	31	30	23	20	34	47	28						26	24	32		

.	18	83**	.	.
.	18	83**	.	.
.	0.1	21	83**	7	.
.	14	67**	.	.
.	14	67**	.	.
.	25	67**	.	.
.	25	83**	7	13
.	.	0.5	18	67**	7	.
.	11	50**	.	.
.	11	50**	.	.
.	11	50**	.	.
.	11	50**	.	.
.	.	0.7	1	21	67**	14	.
.	0.01	1	21	67**	14	.
1	5	0.2	36	83**	36	.
0.1	.	1.5	.	.	0.01	29	67*	29	.
10	.	.	0.5	4	29	67*	29	.
.	7	33*	.	.	
.	7	33*	.	.	
.	13	33*	.	.	
.	13	33*	.	.	
.	13	33*	.	.	

Plot ID	Order 1						Order 2					
	VSR01NW	VSR01SE	VSR02I	VSR022	VSR028	VSR029	VSR02NW	VSR02SE	VSR03NW	VSR005	VSR006	VSR007
Non-vascular plants treated?	Y	Y	Y	Y	Y	Y	Y	Y	Y	N	N	N
Order 2: Festucetalia valesiacae												
Veronica verna	0.01	0.5	0.001	.	0.1	0.005
Poa bulbosa	0.1	1	0.05	.	2	0.01
Dianthus carthusianorum subsp. carthusianorum	10	0.5	0.05	0.1	2	0.5
Arabis nova	0.5
Thymus praecox subsp. polytrichus	5	6	.	.	.
Peucedanum oreoselinum	0.01	0.1	0.01	0.5	.	.
Pulsatilla montana	1	1	0.05	.	.	0.5
Festuca valesiaca	0.3	.	15	65	27	18	15	55
Potentilla pusilla	1.5	1	.	2	.	.	10	5	0.5	1	6	2
Order 3: Brachypodietalia pinnati												
Lathyrus pratensis
Poa angustifolia
Carex pairae
Convolvulus arvensis
Taraxacum officinale aggr.
Veronica chamaedrys
Trifolium alpestre
Achillea millefolium aggr.	0.02	0.5
Bunium bulbocastanum	0.1	0.01	.	.	0.005	0.5
Galium verum	0.1	0.01
W Fraxinus excelsior
W Prunus avium
W Acer campestre
Arrhenatherum elatius
Sanguisorba minor	.	.	0.1
Companion species												
Phleum phleoides	.	.	1	.	0.5	1	3	1.5	0.5	0.75	.	.
Bromus erectus	2	6	0.4	0.5	.	.	.	0.05	30	.	.	.
Galium lucidum	.	0.01	0.7	0.05	.	0.1	0.1	.	0.01	0.1	.	1
Helianthemum nummularium subsp. obscurum	0.1	0.5	0.5	0.5	.	2	.	0.02	0.01	.	.	.
Muscari comosum	.	.	0.05	0.1	0.5	10
Teucrium chamaedrys	1	0.5	10	3	5	.	.	0.01	0.1	0.1	.	.
Stachys recta	0.1	.	0.01	.	0.2	0.01	0.3	.	.	.	0.1	.
Euphorbia cyparissias	.	.	0.1	.	.	4	.	.	.	1	1	3
Arenaria serpyllifolia	0.3	0.05	0.5	0.3	.	.	0.001	.	.	0.01	.	1
Carex caryophyllea	1	10	3	.	.	.
Centaurea scabiosa subsp. scabiosa	0.1	.	.	0.2	.	.	.	0.5
Potentilla argentea	0.001	.	0.1	1	1
Vicia angustifolia	2
Geranium sanguineum	0.1	.	0.01
Koeleria macrantha	0.1	1	0.5	0.5	.	.	.
W Rosa spec.	0.1	.	15
Arabis glabra	0.1	0.5
Elymus hispidus	.	.	3	.	2
Linaria angustissima	0.1
Lotus corniculatus	0.01
Artemisia absinthium	1	15	3

VSR008	Order 2							Order 3							All	O. 1	O. 2	O. 3																	
	N	Z	VSR009	N	VSR012	Y	VSR020	Y	VSR023	Y	VSR025	Y	VSR026	Y	VSR027	Y	VSR03SE	Y	VSR001	Y	VSR002	Y	Z	VSR003	N	VSR004	N	VSR010	N	VSR011	N	VSR024	Y		
2	8	0.05	0.001	0.001	39	17	71**		
0.1	0.5	2	32	17	57*		
0.1	.	.	8	0.1	2	1	1	1	0.01	.	.	0.1	4	.	0.05	.	0.01	0.1	4	.	0.05	.	61	17	86*	50	
.	2	0.01	.	0.01	14	.	29*		
.	.	0.5	2	14	.	29*		
0.1	.	0.05	.	0.5	2	.	.	0.5	2	36	17	57*	13	
15	3	0.3	0.3	1	0.2	36	17	57*	13
70	30	15	20	1	50	80	70	2	20	25	30	20	35	5	82	33	100*	88	
5	3	2	.	0.3	2	5	5	0.2	.	5	.	0.1	.	.	0.1	.	0.1	0.1	0.1	0.1	75	67	93*	50	

.	.	0.05	0.1	0.5	0.5	.	0.5	0.5	4	0.1	0.1	0.5	0.5	4	0.1	29	.	7	88**	.					
.	2	0.05	0.2	2	3	.	10	20	0.05	5	.	32	.	21	75**		
.	5	8	.	.	0.5	5	.	14	.	.	50**		
.	2	0.5	.	0.1	0.2	.	.	14	.	.	50**		
.	0.5	0.5	.	0.1	1	.	.	14	.	.	50**		
.	1	.	.	.	1	0.5	4	14	.	.	50**		
2	7	.	4	0.2	0.1	3	14	8	10	.	7	36	.	29	75**	
.	3	.	0.2	0.2	0.2	15	10	.	.	5	18	0.2	39	.	36	75*
0.1	4	2	0.001	0.1	4	2	.	39	.	36	75*	
.	3	0.1	0.2	.	10	6	0.1	.	10	1.5	0.2	39	.	36	75*	
.	.	2	0.001	0.01	0.5	.	.	.	0.05	.	18	.	7	50*	
.	.	.	0.1	0.01	4	.	0.5	.	0.3	.	18	.	7	50*		
.	1	0.001	.	8	.	.	11	.	.	38*		
.	0.1	1	0.5	.	11	.	.	38*	
.	.	0.1	0.5	0.5	.	.	0.1	0.1	0.05	.	25	17	7	63*	

0.1	3	1	5	0.2	2	0.5	2	.	1	4	5	4	5	0.1	.	75	50	86	75	
.	25	20	12	2.5	0.1	5	2	40	20	15	40	60	15	1	.	71	67	64	88	
.	2	3	0.5	0.2	6	.	.	10	1	.	54	67	57	38		
0.1	.	.	0.3	.	0.5	0.3	0.1	0.05	0.1	50	83	43	38
0.1	.	.	.	0.1	0.01	0.3	0.1	.	0.1	2	0.3	0.5	0.1	1	.	50	17	50	75	
.	3	0.01	.	.	0.2	.	.	0.2	0.1	.	46	83	43	25	
0.1	1	0.5	.	0.3	0.3	0.5	43	67	50	13	
0.1	.	0.05	.	0.3	2	.	5	2	.	.	.	39	33	43	38	
0.1	.	.	0.1	0.01	36	67	36	13	
8	1	.	.	.	8	3	.	.	3	0.5	7	36	.	50	38	
.	.	.	0.2	0.2	0.1	0.2	.	0.5	4	.	.	32	33	36	25	
0.1	2	2	.	0.1	0.5	.	32	.	36	50		
0.1	8	0.05	.	.	.	0.1	.	0.5	.	0.1	0.1	0.2	.	.	32	.	36	50	
.	5	4	12	3	5	.	2	.	.	29	17	29	38	
0.1	2	4	0.1	29	17	43	13	
.	5	3	0.01	.	5	.	.	15	0.5	.	29	.	29	50	
.	3	0.01	0.5	.	45	15	.	0.2	0.5	.	25	33	7	50	
0.01	.	0.05	0.1	.	0.05	.	.	0.001	.	0.1	.	5	0.2	.	25	.	21	50	
0.1	.	.	.	0.001	.	0.1	.	0.1	.	5	0.2	.	.	1	.	25	.	21	50
.	.	0.3	25	2	.	21	.	29	25

Plot ID	Order 1						Order 2					
	V01NW	V01SE	V02I	V022	V028	V029	V02NW	V02SE	V03NW	V005	V006	V007
Non-vascular plants treated?	Y	Y	Y	Y	Y	Y	Y	Y	Y	N	N	N
Artemisia campestris	.	.	3	.	6	2	.	.	.	4	.	.
Carex humilis	15	5	.	0.7	1	.	.	.
Hieracium pilosella	2	0.01	.	.	.
Hypericum perforatum	0.01	.	0.01
B Syntrichia ruralis	.	.	.	0.05	1	0.5	.	0.1
Trifolium arvense	0.1	.	0.01	0.001	.	.	0.01	0.5
B Bryum sp.	0.2	.	0.1
B Ceratodon conicus	5.7
B Weissia sp.	.	0.1	0.1
Carduus nutans	0.01	0.1	.
Chondrilla juncea	0.5	.	.	0.1	0.5	.
Sedum rupestre aggr.	0.05	.	.	.	1	.	1
Dactylis glomerata
Knautia arvensis
Ranunculus bulbosus
Silene nutans	.	.	0.3
Trifolium montanum
Vicia hirsuta	0.5
B Abietinella abietina	.	.	0.01
L Cladonia novochlorophaea	0.2
B Rhytidadelphus triquetrus	.	.	.	0.01
Berberis vulgaris
Brachypodium rupestre	8	.	.	.
Bromus tectorum	.	.	0.2	.	0.2
Erysimum rhaeticum	.	0.01	.	.	.	0.01
Pimpinella saxifraga aggr.	1	.	.	.
Salvia pratensis	0.5	.	.	.
Sedum montanum	.	.	0.5	.	0.3
Agrostis capillaris
Anthoxanthum odoratum
Aster linosyris	6
Briza media
Calamagrostis epigejos
Campanula rotundifolia	0.1	.	.	.
Carlina vulgaris aggr.
Cirsium arvense
Clinopodium vulgare
Jasione montana
Koeleria pyramidata
Lactuca perennis
Ononis natrix	.	.	.	0.2
Orchis cf. morio
Origanum vulgare
Petrorhagia prolifera	0.01	0.1	.	.
Plantago media
W Populus tremula
W Rhamnus cathartica
W Rubus fruticosus aggr.

Z	VSR008	Order 2							Order 3							All	O. 1	O. 2	O. 3																		
		Z	VSR009	Z	VSR012	Y	VSR020	Y	VSR023	Y	VSR025	Y	VSR026	Y	VSR027	Y	VSR03SE	Y	VSR001	Y	VSR002	Y	Z	VSR003	Y	Z	VSR004	Y	Z	VSR010	Y	Z	VSR011	Y	VSR024		
1	.	.	15	21	50	21	21	50	21	.	.	
.	.	.	.	40	0.1	21	50	14	13	21	50	14	13	.	
.	0.02	.	.	0.02	.	0.5	.	0.05	.	0.05	.	0.05	.	10	.	.	.	12	.	21	.	21	.	21	38	.	.	21	17	14	38	.
.	0.01	0.05	0.4	0.5	.	.	21	17	14	38	21	50	38	.	.		
.	.	0.02	0.2	21	50	38	21	17	36	.	.		
.	0.01	.	.	.	0.01	19	17	25	19	17	25	.	.			
.	0.01	.	.	.	0.9	0.9	.	.	.	19	17	25	19	17	25	.	.			
.	0.01	.	.	0.01	0.01	.	.	.	19	17	25	19	17	25	.	.				
.	0.4	0.3	.	.	.	0.3	1	.	.	18	.	21	25	18	.	21	25	.	.			
.	0.4	0.4	.	.	.	18	.	29	13	18	.	29	13	.	.			
1	.	0.01	18	17	29	18	17	29	.	.			
.	1	0.1	0.05	0.1	14	.	7	38	14	.	7	38	.	.				
.	.	.	0.1	0.1	1	.	0.1	0.2	14	.	7	38	14	.	7	38	.	.			
0.1	3	0.1	0.1	.	.	.	14	.	7	38	14	.	7	38	.	.		
.	.	.	1	1	2	14	17	7	25	14	17	7	25	.	.		
1	0.5	0.1	0.1	0.2	14	.	21	13	14	.	14	25	.	.		
.	0.01	0.5	.	0.1	.	.	.	0.5	0.1	14	.	14	25	13	17	13	.	.			
.	0.08	0.08	13	17	13	13	17	13	.	.	.				
.	0.9	0.9	13	17	13	13	17	13	.	.	.				
.	9	13	17	.	25	.	.	.	9	13	17	.	25	.	.			
.	10	2	0.1	11	.	14	13	11	.	14	13	.	.			
.	0.05	40	0.05	11	.	14	13	11	33	7	.	.	.			
.	.	0.2	0.2	11	33	7	11	33	7	.	.	.				
0.1	3	3	0.5	11	.	7	25	11	33	7	.	.	.			
.	0.1	.	0.05	0.1	0.05	11	.	14	13	11	33	7	.	.	.			
.	.	.	1	1	11	33	7	11	33	7	.	.	.				
.	0.2	0.2	10	7	.	.	25	.	.	.	10	7	.	.	25	.	.				
.	0.1	.	0.1	0.1	5	7	.	.	25	.	.	.	5	7	.	.	25	.	.				
0.1	0.1	.	0.1	0.1	7	17	7	7	17	7				
.	0.1	.	0.1	0.1	10	7	.	.	25	.	.	.	10	7	.	.	25	.	.				
.	0.1	.	0.1	0.1	7	17	7	.	25	.	.	.	7	17	7	.	25	.	.				
.	0.1	.	0.1	0.1	.	.	.	0.2	.	.	7	.	25	.	.	.	7	17	7	.	25	.	.				
.	.	.	0.01	0.2	0.1	.	.	.	3	.	.	7	.	25	.	.	.	7	17	7	.	25	.	.				
.	4	.	.	.	0.2	0.2	.	.	.	0.2	.	.	7	.	14	.	.	.	7	17	7	.	13	.	.				
0.1	.	.	.	0.2	0.2	.	.	.	0.2	.	.	7	.	14	.	.	.	7	17	7	.	13	.	.				
0.1	.	.	.	0.2	.	.	.	0.05	0.05	.	.	.	0.05	.	.	7	.	14	.	.	.	7	17	7	.	13	.	.				
.	.	.	.	0.2	.	.	.	0.05	0.05	.	.	.	0.05	.	.	7	.	14	.	.	.	7	17	7	.	13	.	.				
.	.	.	.	0.2	.	.	.	0.1	0.1	.	.	.	0.2	.	.	7	.	13	.	.	.	7	17	7	.	13	.	.				
.	.	.	.	0.2	.	.	.	0.2	0.2	.	.	.	0.3	.	.	7	.	7	.	.	.	7	17	7	.	13	.	.				
.	.	.	.	0.2	.	.	.	0.5	0.5	.	.	0.01	7	.	.	25	7	17	7	.	25	.	.					
.	7	0.1	0.1	.	.	.	10	.	.	7	.	7	.	.	.	7	17	7	.	13	.	.				

Plot ID	Order 1						Order 2					
	V01NW	V01SE	V021	V022	V028	V029	V02NW	V02SE	V03NW	V005	V006	V007
Non-vascular plants treated?	Y	Y	Y	Y	Y	Y	Y	Y	Y	N	N	N
Sedum telephium subsp. maximum	4
Sorbus aria
Teucrium montanum	.	0.25
Thymus pulegioides subsp. carniolicus
Thymus pulegioides subsp. pulegioides
Tragopogon dubius	0.01
Trifolium pratense subsp. pratense
Trifolium repens
Verbascum lychnitis	0.5	0.01	.	.
Veronica arvensis
Vicia cracca
Vicia cracca subsp. incana	0.1
Viola hirta
B Brachythecium cf. glareosum	.	.	0.7
B Brachythecium glareosum
L Cladonia cariosa
L Cladonia pyxidata aggr.	0.01
B Grimmia laevigata	0.1
L Leptogium gelatinosum	.	.	0.05
B Phascum cuspidatum
B Trichostomum crispulum	.	.	0.025
Allium sphaerocephalon	.	.	0.01
Allium vineale
Asplenium adiantum-nigrum
Asplenium trichomanes
Astragalus exscapus
Astragalus onobrychis	0.1
W Betula pendula
Bothriochloa ischaemum	25	.	.	.
Campanula scheuchzeri
Campanula spicata	.	.	0.2
cf. Astragalus sp.	.	.	0.1
cf. Erigeron acris
cf. Filago arvensis	1
cf. Picris hieracioides	0.1
W Cornus sanguinea
Crupina vulgaris	.	0.01
Daucus carota	0.01	.	.	.
Elymus repens
Erigeron acris
Festuca cf. guestfalica
Fragaria vesca
Fumana procumbens	.	0.05
Galium pumilum
Geum urbanum
Globularia bisnagarica
Globularia cordifolia	.	.	.	0.1
Helictotrichon pubescens

		Order 2							Order 3						All	O. 1	O. 2	O. 3																		
Z	VSR008	Z	VSR009	Z	VSR012	Y	VSR020	Y	VSR023	Y	VSR025	Y	VSR026	Y	VSR027	Y	VSR03SE	Y	VSR001	Y	VSR002	Y	Z	VSR003	Y	Z	VSR004	Y	Z	VSR010	Y	Z	VSR011	Y	VSR024	Y
.	.	.	.	4	7	17	7	.	.	.						
.	25	0.1	.	.	7	.	.	7	13			
.	.	.	.	0.5	7	17	7		
.	.	.	.	0.5	1	6	.	7	.	.	7	13	
.	0.1	.	.	.	2	.	.	7	.	.	7	25	
.	0.1	0.5	.	7	.	.	7	13	
.	0.2	0.1	.	7	.	.	7	25	
.	0.1	7	.	.	7	14
0.1	0.1	7	.	.	7	13	
.	3	1	7	.	.	7	13	
.	.	.	.	0.5	0.05	.	.	0.1	7	17	7	.	.	.	25
.	0.05	6	17	25
.	.	.	.	0.1	0.1	1	6	.	.	.	13		
.	0.1	6	.	13	.	.	.	13	
.	0.005	6	17	.	.	.	6	17	
.	0.005	6	.	13	.	.	.	13	
0.1	0.3	4	.	.	7	.	.	13
.	0.05	4	.	.	4	.	.	13	
.	.	.	.	1	1	4	.	17	.	.	.	13	
.	50	4	.	.	.	13			
.	0.1	4	.	7	.	.	13		
.	0.001	4	17	.	.	.	13		
.	0.001	4	17	.	.	.	13		
.	0.05	4	17	.	.	.	7		
.	0.05	4	17	.	.	.	7		
.	0.05	4	4	.	.	.	13		
.	1	4	4	.	.	.	13		
.	1	10	4	.	.	.	13		
.	1	0.5	4	.	.	.	13		
.	0.2	4	17	.	.	.	13		
.	.	.	.	1	1	0.05	.	4	.	.	13		
.	.	.	.	1	1	4	4	.	.	.	7		
.	.	.	.	1	1	4	17	.	.	.	7		
.	.	.	.	3	3	.	4	3	4	.	.	.	13		

Plot ID	Order 1						Order 2					
	VSR01NW	VSR01SE	VSR021	VSR022	VSR028	VSR029	VSR02NW	VSR02SE	VSR03NW	VSR005	VSR006	VSR007
Non-vascular plants treated?	Y	Y	Y	Y	Y	Y	Y	Y	Y	N	N	N
Hieracium umbellatum
Hieracium velutinum
Holcus lanatus
Hypochaeris maculata
W Juniperus sabina
Knautia dipsacifolia
Leontodon hispidus
Lithospermum arvense
Medicago sativa
Oxytropis pilosa	.	.	0.2
Plantago lanceolata
Poa cf. perconcinna	0.01
Poa pratensis
Polygonatum odoratum
Polygonum aviculare aggr.
Potentilla rupestris	.	.	.	10
Prunella grandiflora
W Prunus avium
W Prunus cerasifera
Ranunculus polyanthemophyllus
W Rubus canescens
Saponaria ocymoides
Scleranthus perennis
Sedum sexangulare
Selseria caerulea	.	.	0.3
Sempervivum arachnoideum	1	.	.	.
Sempervivum montanum	.	.	0.7
Setaria viridis	0.5	.	.	.
Silene viscaria
W Sorbus aria
Stipa pennata aggr.	0.1	.	.	.
Thalictrum minus
Thymus pulegioides	1	.	.	.
Tragopogon pratensis
Trifolium medium
Trifolium rubens
Urtica dioica
Verbascum thapsus	0.5	.	.
Veronica dillenii	.	.	.	0.1
Veronica praecox	.	.	0.001
Veronica teucrium

