

Dry grassland vegetation in the Transcarpathian Lowland (western Ukraine)

Trockenrasenvegetation im Transkarpatischen Tiefland (West-Ukraine)

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Abstract

The Transcarpathian Lowland in the Zakarpattia Oblast (western Ukraine) is the north-easternmost extension of the Pannonian Basin. The vegetation survey in this area has so far focused on mesic grasslands and forests, whereas dry grassland vegetation has been poorly known. Therefore, we performed a survey of the dry grassland sites in this area, recorded species composition in vegetation plots ($n = 45$) and classified them using agglomerative clustering. Results were summarised in comparative tables of species composition and environmental characteristics and by using NMDS ordination. Dry grasslands in this area occur mainly on volcanic hills with acidic andesite bedrock. Four associations were distinguished: (i) semi-dry grasslands with *Brachypodium pinnatum* (*Scabioso ochroleucae-Brachypodium pinnati*, alliance *Cirsio-Brachypodium pinnati*), (ii) volcanic slope steppes with *Festuca pseudodalmatica* (*Festucetum pseudodalmaticae*, alliance *Festucion valesiacae*), (iii) acidophilous dry grasslands with *Festuca stricta* subsp. *sulcata* and forest-fringe specialists (*Astero linosyris-Festucetum rupicolae*, alliance *Koelerio-Phleion phleoidis*) and (iv) nutrient-poor acidophilous grasslands with *Vulpia myuros* (*Airo-Vulpietum*; alliance *Thero-Airion*). Except for the *Scabioso-Brachypodium*, which has already been reported from the Upper Tysa valley, all of these associations are new to Ukraine. We characterise these associations and describe the most remarkable sites of dry grasslands in the Transcarpathian Lowland: Chornahora Hill near the town of Vynohradiv, the Mukacheve Hills, the Berehove Hills and slopes above the Uzh River valley near the village of Onokivtsi. We also discuss their environmental conditions and conservation issues.

Keywords: *Cirsio-Brachypodium pinnati*, dry grassland, *Festucion valesiacae*, *Festuco-Brometea*, *Koelerio-Phleion phleoidis*, phytosociology, *Thero-Airion*, vegetation classification, vegetation survey

Erweiterte deutsche Zusammenfassung am Ende des Artikels

1. Introduction

Dry grasslands are a physiognomically and ecologically distinct type of vegetation. They are formed of herbaceous plants, mostly grasses, and inhabit dry sites on both shallow and deep soils. Dry grasslands of the class *Festuco-Brometea* form the natural zonal vegetation

in the steppe biome from Central-Eastern Europe to Central Asia (DENGLER et al. 2014). The Pannonian Basin is considered to be the westernmost large exclave of the Eurasian forest-steppe biome (ERDŐS et al. 2018). However, the origin and history of the Pannonian steppes is complicated and still not completely understood. Recent palaeoecological studies suggest some of them to be relics of the late-Pleistocene steppe (MAGYARI et al. 2010, KUNEŠ et al. 2015, JAMRICOVÁ et al. 2017), harbouring steppe species throughout the entire Holocene. Human impact on the landscape resulted in the creation of various secondary habitats, while at the same time livestock grazing, mowing for hay or burning contributed to the maintenance of natural grasslands (POSCHLOD et al. 2009, HEJCMAN et al. 2013). Many grassland types dependent on human management are nowadays threatened by abandonment (LERMAN et al. 2004, VALKÓ 2016), which causes losses of both species and habitat diversity (LERMAN et al. 2004). Therefore, dry grasslands are protected on the European level. Most of the natural and semi-natural grasslands are included in the Habitats Directive of the European Union (COUNCIL OF EUROPEAN COMMUNITIES 1992), and several types of dry grasslands were considered as threatened in the European Red List of Habitats (JANSSEN et al. 2016) and in the habitat list of the Resolution 4 of the Bern Convention, which is used as a conservation instrument in Ukraine (ANONYMOUS 2014).

Species composition and vegetation types of Central European dry grasslands have been studied extensively since the 1920s, and there is a wealth of data and knowledge. In the last decades, national synthetic studies of this vegetation were completed for some countries, e.g. Austria (MUCINA & KOLBEK 1993), the Czech Republic (CHYTRÝ et al. 2007), Hungary (BORHIDI et al. 2012), Slovakia (JANIŠOVÁ et al. 2007, ŠKODOVÁ et al. 2014) and Romania (COLDEA & SÂRBU 2012). The grasslands of the class *Festuco-Brometea* have recently been classified internationally at a higher level of syntaxonomic classification (WILLNER et al. 2017), and those of the order *Brachypodietalia pinnati* at the association level across Central and Eastern Europe (WILLNER et al. 2019). Despite this long research tradition and recent efforts at synthesis, there are still areas in which our knowledge of this vegetation is insufficient. One of them is the Transcarpathian (Tysa) Lowland in the north-eastern part of the Pannonian Basin, in the Zakarpattia Oblast (= Transcarpathian Region) of western Ukraine (compare WILLNER et al. 2017, 2019).

The flora of this area was actively studied by Hungarian botanists (e.g. A. Boros, A. Margittai and Z. Thaisz), especially at the beginning of the 20th century, when it was part of the Austro-Hungarian Empire. Later on, when the area became part of Czechoslovakia (1918–1938), Czech botanists (e.g. J. Buček, M. Deyl, K. Domin, M. Pulchart and A. Zlatník) continued studies of flora, but also started vegetation studies. Most of their work was related to the Eastern Carpathians and their foothills (KOBIV 2016), focusing on forests and subalpine areas. Nevertheless, they also briefly mentioned some sites of dry grasslands in the Transcarpathian Lowland: DOMIN (1937) reports *Festucetum pseudodalmaticae* vegetation in southernmost Transcarpathia and PULCHART (1937) *Stipetum pulcherrimae* vegetation on the Chornahora Hill near the town of Vynohradiv. Vegetation research during the Soviet period (1945–1991) was insignificant, and phytosociological studies in the post-Soviet period focused mostly on forests (e.g. ONYSHCHENKO & LUKASH 2005, NOVÁK et al. 2017) and traditionally managed mesic grasslands (ŠKODOVÁ et al. 2015, ZAJAC et al. 2016). The presence of dry grassland vegetation in this area was recently also mentioned in a handbook of habitats of the Transcarpathian Lowland (KISH et al. 2006), in the Red Data Book of Ukraine (DIDUKH 2009) and the National Habitat Catalogue of Ukraine (KUZEMNKO et al. 2018).

Here, our aim is to close the gap in knowledge of dry grassland vegetation in the Transcarpathian Lowland, with three objectives: (1) to explore the current distribution of dry grasslands in the area, (2) to classify them at the association level and (3) to describe their most remarkable sites and threats.

2. Study area

The Transcarpathian (Tysa) Lowland (Fig. 1) occupies the south-western part of the Zakarpattia Region (Oblast) of Ukraine, extending in northwest-southeast direction from the town of Uzhhorod to the town of Vynohradiv. It lies between the western foothills of the Eastern Carpathian Mountains and the state borders of Slovakia, Hungary and Romania. The total area of the Transcarpathian Lowland is about 2,000 km². Being situated on the south-western side of the Eastern Carpathians, its flora and vegetation are biogeographically linked to that of the Pannonian (Carpathian) Basin rather than to the rest of the Ukrainian territory (DIDUKH & SHEL'YAG-SOSONKO 2003). Miocene sediments predominate in the area, being covered by loess at a few sites near its eastern edge. Tertiary volcanic (predominantly andesite, but also dacite and rhyolite; PÉCSKAY et al. 2000) hills rise from the lowland in several places, including Chornahora Hill near Vynohradiv, the Mukacheve Hills and the hill in the village of Siltse. The average altitude of the lowland is between 100 and 120 m a.s.l. It is



Fig. 1. Map of the Transcarpathian Lowland showing sample plots (relevés) and their classification to associations.

Abb. 1. Karte des Transkarpatischen Tieflandes mit Lage der Vegetationsaufnahmen und ihrer Zugehörigkeit zu Assoziationen.

Table 1. Climatic characteristics of the study sites in different regions within the study area. Mean, minima and maxima of mean annual temperature, total annual precipitation (from WorldClim ver. 2) and altitude for the relevé sites are given. Regions are defined ad hoc as spatial clusters of sampled sites. The assignments of individual relevés to a region are indicated in Supplement E2.

Tabelle 1. Klima der betrachteten Untersuchungsgebiete. Mittlere, minimale und maximale Jahrestemperaturen sowie Jahresniederschläge (aus WorldClim ver. 2) sowie die Meereshöhen sind angegeben. Die Zugehörigkeit der Vegetationsaufnahmen zu den ad hoc definierten Untersuchungsgebieten findet sich in der Anhang E2.

Region	Temperature (° C)			Precipitation (mm)			Altitude (m a.s.l.)		
	mean	min.	max.	mean	min.	max.	mean	min.	max.
Berehove	9.6	9.5	9.7	751	731	771	172	125	208
Mukacheve	9.5	9.4	9.6	836	807	846	234	213	261
Uzhhorod	9.1	8.7	9.5	788	763	806	171	136	214
Vynohradiv	9.5	9.3	9.6	934	874	967	218	142	335
All sites	9.4			851			202		

drained by four main rivers, Uzh, Latorytsia, Borzhava and Tysa. Upstream, in the Carpathian foothills, these rivers flow in relatively narrow valleys, which are devoid of dry grasslands except the Uzh and Tysa valleys.

The climate of the Transcarpathian Lowland is relatively warm and humid, reflecting its position at the transition between the dry and continental Pannonian Basin and the wet and cool Carpathians. Based on the data from the WorldClim ver. 2 database (FICK & HUMANS 2017), the mean annual temperature of the lowland is approximately 9.4 °C, while the total annual precipitation is about 850 mm (Table 1). Precipitation increases steeply towards the Carpathian foothills, which do not support dry grasslands of the class *Festuco-Brometea*. Nevertheless, even in the lowland, the presence of this vegetation type is confined to sites with locally drier topoclimate and soil conditions.

Most of the Transcarpathian Lowland is covered by arable land, while approximately 15% of the area is covered by oak-hornbeam, floodplain and beech forests, the latter occurring especially on the north-facing slopes of volcanic hills. The south-facing slopes of several volcanic hills in the southern part of the area are covered by abandoned or actively used vineyards.

3. Methods

3.1 Data

We sampled dry grassland vegetation in the Zakarpattia Oblast in June 2016 and May 2017. We defined the focal vegetation in the field based on its grassland physiognomy, presence of species typical of dry grasslands (e.g. *Brachypodium pinnatum*, *Festuca pseudodalmatica*, *F. stricta* subsp. *sulcata* [syn. *F. rupicola*] and *F. valesiaca*) and the absence of species typical of *Nardus stricta* grasslands (e.g. *Agrostis capillaris*, *Nardus stricta* and *Viola canina*), which occupy topographically similar sites deeper in the Carpathian foothills. Vegetation was sampled using relevés, i.e. square plots of 16 m², in which covers of individual species were estimated using the nine-degree Braun-Blanquet cover-abundance scale (WESTHOFF & VAN DER MAAREL 1973). We recorded all species of vascular plants and bryophytes except epilithic species. Lichens were rare, and we did not determine them. For each relevé, we estimated the cover of the shrub, herb and moss layer and the height of shrub and herb layer. Within each plot, we measured soil depth in nine positions using a 35 cm long iron stick, collected soil samples

from a depth of 5–10 cm in four positions for subsequent pH measuring, measured slope aspect and inclination, and recorded geographic coordinates using a GPS device. The altitude of sites was extracted from a digital topographical model (JARVIS et al. 2008) using the R *raster* 2.7 package (HIJMANS 2017). Heat load index and radiation index were calculated from slope aspect and inclination using a formula of MCCUNE & KEON (2002: Eq. 3).

We collected some vascular plants and bryophytes for further determination or revision. The specimens of vascular plants are stored in the herbarium of Masaryk University in Brno (BRNU) and bryophytes in the personal herbarium of K. Chytrý and the herbarium of the Moravian Museum in Brno (BRNM). We also collected individuals of the *F. valesiaca* group in order to distinguish *F. valesiaca* s.str. (2n = 14) and *F. pseudodalmatica* (2n = 28; ŠMARDÁ et al. 2005) using flow cytometry.

The nomenclature of vascular plants follows the Euro+Med PlantBase (<http://ww2.bgbm.org/EuroPlusMed/>; accessed 2018-08-31) except for the genus *Thymus*, which follows DANIHELKA et al. (2012). The nomenclature of bryophytes follows HODGETTS (2015). Specimens determined only at the genus level were excluded from the dataset in all cases where they may have included more than one species. *Weissia* species (fertile or sterile) without inner capsule were reported in the dataset as *Weissia* spp., while *W. longifolia* was recognised separately. *Erigeron annuus* and *E. strigosus* were merged into *E. annuus* agg., *Poa angustifolia* and *P. pratensis* into *P. pratensis* agg., *Thymus pannonicus* and *T. × porcii* into *T. pannonicus* agg., *Veronica dillenii* and *V. verna* into *V. verna* agg. Aggregates in the genera *Luzula*, *Rosa* and *Rubus* follow the definitions of DANIHELKA et al. (2012).

3.2 Data analysis

The relevés were stored in a Turboveg 2 database (HENNEKENS & SCHAMINÉE 2001) and analysed using Juice 7.0 (TICHÝ 2002) and R (R CORE TEAM 2017) with the *tidyverse* package (WICKHAM 2017). For the data analysis, we used the ordinal cover scale in which the nine degrees of the Braun-Blanquet scale were replaced by the numbers 1–9. The dataset was classified using the complete-linkage algorithm and the Bray-Curtis dissimilarity index. This clustering method was chosen using the OptimClass 2 approach (TICHÝ et al. 2010). Measured environmental variables and Borhidi indicator values (BORHIDI 1995) were used to assess ecological differences between the relevé clusters. Analysis of variance (ANOVA) and subsequent Tukey’s post-hoc tests were performed using the R *stats* package (R CORE TEAM 2017) to test statistical differences between clusters. Borhidi indicator values were compared using a modified permutation test (ZELENÝ & SCHAFFERS 2012) and subsequent multiple t-test comparisons. Moreover, ordination was computed using non-metric multidimensional scaling (NMDS), and the best-fitted species were displayed in the ordination diagram. To fit the species, we used the *envfit* function of the R package *vegan* (OKSANEN et al. 2017).

Fidelity of species to relevé groups was assessed using the phi coefficient of association (SOKAL & ROHLF 1995), which was calculated with virtually equalised sizes of relevé groups. Species with a phi coefficient higher than 0.5 were considered as diagnostic except for the rare species with non-significant ($p \geq 0.05$) association with the relevé group as detected using Fisher’s exact test (TICHÝ & CHYTRÝ 2006). Constant species were defined as those occurring in at least half of the group’s relevés. The threshold for dominant species was a cover value > 15% occurring in more than 10% of the plots.

4. Results

We recorded 296 taxa of vascular plants and 43 taxa of bryophytes (i.e. 339 in total, including the taxa determined only to the genus level). The dataset contained many drought-tolerant species that are also acidophilous or acidotolerant. The most frequent species (present in more than half of the relevés) were *Arenaria serpyllifolia*, *Cerastium brachypetalum*, *Erigeron annuus* agg., *Poa pratensis* agg., *Potentilla argentea* and *Trifolium arvense*. For the full table of relevés see Supplement E1.

4.1 Classification of the dry grasslands

We determined four clusters, which resulted from the cluster analysis, and interpreted them as phytosociological alliances: (i) semi-dry grasslands with *Brachypodium pinnatum* (*Cirsio-Brachypodion pinnati*), (ii) volcanic slope steppes with *Festuca pseudodalmatica* (*Festucion valesiacae*), (iii) acidophilous forest-fringe vegetation with *Festuca stricta* subsp. *sulcata* and forest-fringe specialists (*Koelerio-Phleion phleoidis*) and (iv) nutrient-poor acidophilous grasslands with *Vulpia myuros* (*Thero-Airion*; Table 2). These clusters were superimposed on the ordination diagram (Fig. 2a).

The environmental data were averaged for each cluster group and are shown together with average Borhidi indicator values in Table 3. The results of the Tukey's post-hoc test indicate that the most sharply separated association is *Scabioso-Brachypodietum*, which occurs on deeper soils supporting the development of a denser herb layer. The other vegetation types are connected by various transitional forms.

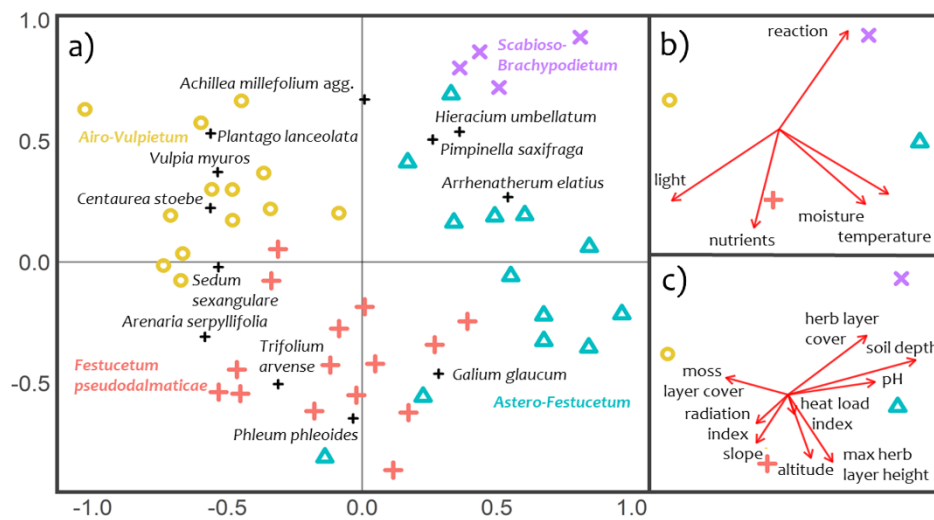


Fig. 2. NMDS ordination diagram showing sites and the species with the best fit. **a)** The stress of the analysis is 0.21. The fitted vectors include **b)** Borhidi indicator values for light, temperature, moisture, reaction and nutrients and **c)** geographic and topographic variables (altitude, heat load index, radiation index, slope, soil depth and pH) and vegetation characteristics (herb and moss layer cover and herb layer height). Both vector plots (b, c) also display the centroid of relevés classified to individual associations. Missing values of soil pH ($n = 5$) and herb layer height ($n = 4$) were replaced by the mean values of vegetation types in vector fitting.

Abb. 2. NMDS-Ordination: **a)** Darstellung von Aufnahmen und Arten mit dem besten Fit (Stress = 0,21). Projektion der Vektoren für **b)** die Borhidi-Zeigerwerte und **c)** für geografische und topografische Variablen sowie Strukturparameter in das Ordinationsdiagramm zusammen mit den Zentroiden der Assoziationen. Fehlende Werte für den Boden-pH ($n = 5$) und die Krautschichthöhe ($n = 4$) wurden für die Projektion durch die jeweiligen Assoziationsmittelwerte ersetzt.

Table 2. Shortened synoptic table with diagnostic species of the associations *Scabioso-Brachypodietum* (S-B), *Festucetum pseudodalmaticae* (Fp), *Astero-Festucetum* (A-F) and *Airo-Vulpium* (A-V) and with other common species. The values in the table are species percentage constancies. Shaded species are ranked by decreasing fidelity to individual associations: Dark shading is used for $\phi \geq 0.6$ and light shading for $0.6 > \phi \geq 0.5$. Bryophytes are indicated with (B). A full version of the data table with individual relevés and complete species lists is available in Supplement E1.

Tabelle 2. Gekürzte Stetigkeitstabelle (%) mit den diagnostischen Arten der Assoziationen *Scabioso-Brachypodietum* (S-B), *Festucetum pseudodalmaticae* (Fp), *Astero-Festucetum* (A-F) und *Airo-Vulpium* (A-V) sowie weiteren häufigen Arten. Diagnostische Arten sind nach fallenden phi-Werten sortiert, wobei dunkelgrau für $\phi \geq 0,6$ und hellgrau für $0,6 > \phi \geq 0,5$ steht. Eine ungekürzte Tabelle mit den Einzelaufnahmen und allen Arten findet sich in Anhang E1.

Association	S-B	Fp	A-F	A-V
Number of relevés	4	15	13	13
<i>Scabioso ochroleuca-Brachypodietum pinnati</i>				
<i>Carex filiformis</i>	100	.	.	.
<i>Brachypodium pinnatum</i>	100	7	15	.
<i>Agrimonia eupatoria</i>	100	.	15	8
<i>Dactylis glomerata</i>	75	7	.	.
<i>Veronica chamaedrys</i>	75	7	.	.
<i>Medicago sativa</i>	75	.	.	8
<i>Pimpinella saxifraga</i>	100	13	23	15
<i>Viola hirta</i>	75	7	8	.
<i>Ranunculus polyanthemos</i>	75	.	15	.
<i>Centaurea jacea</i>	75	.	15	.
<i>Trifolium montanum</i>	75	.	15	8
<i>Arrhenatherum elatius</i>	100	27	46	.
<i>Allium vineale</i>	50	.	.	.
<i>Ptychostomum rubens</i> (B)	50	.	.	.
<i>Salvia verticillata</i>	50	.	.	.
<i>Galium verum</i>	75	.	15	23
<i>Solidago virgaurea</i>	50	.	8	.
<i>Inula salicina</i>	50	.	8	.
<i>Stachys officinalis</i>	50	.	8	.
<i>Rosa spinosissima</i> juv.	50	.	8	.
<i>Euphorbia cyparissias</i>	100	47	38	15
<i>Festucetum pseudodalmaticae</i>				
<i>Stachys recta</i>	.	53	.	.
<i>Phleum phleoides</i>	.	73	23	8
<i>Cota tinctoria</i>	.	53	8	.
<i>Festuca pseudodalmatica</i>	.	60	.	15
<i>Hylotelephium maximum</i>	.	67	31	.
<i>Teucrium chamaedrys</i>	.	47	.	8
<i>Trifolium arvense</i>	.	93	31	62
<i>Galium glaucum</i>	.	67	38	.
<i>Seseli osseum</i>	.	33	.	.
<i>Valerianella locusta</i>	.	33	.	.
<i>Astero linosyris-Festuceum rupicolae</i>				
<i>Inula ensifolia</i>	.	.	46	.
<i>Peucedanum oreoselinum</i>	.	.	46	.
<i>Galatella linosyris</i>	.	7	46	.
<i>Koeleria macrantha</i>	.	.	46	8
<i>Festuca stricta</i> subsp. <i>sulcata</i>	.	33	69	8
<i>Calamagrostis epigejos</i>	25	13	77	23

Association	S-B	Fp	A-F	A-V
Number of relevés	4	15	13	13
<i>Verbascum chaixii</i> subsp. <i>austriacum</i>	.	.	31	.
<i>Filipendula vulgaris</i>	.	.	31	.
Airo-Vulpietum				
<i>Vulpia myuros</i>	.	7	.	85
<i>Scleranthus annuus</i>	.	7	.	77
<i>Centaurea stoebe</i>	.	20	.	77
<i>Plantago lanceolata</i>	50	7	8	100
<i>Crataegus</i> sp.	.	.	.	54
<i>Bromus hordeaceus</i>	.	.	.	54
<i>Sanguisorba minor</i>	.	.	.	46
<i>Anthemis arvensis</i>	.	7	.	46
<i>Syntrichia ruralis</i> (B)	.	.	.	31
<i>Carex hirta</i>	.	.	.	31
Other species occurring in at least 20% of relevés				
<i>Potentilla argentea</i>	.	73	31	92
<i>Cerastium brachypetalum</i>	.	73	62	46
<i>Arenaria serpyllifolia</i>	.	73	23	85
<i>Erigeron annuus</i> agg.	75	40	62	62
<i>Poa pratensis</i> agg.	100	20	46	77
<i>Weissia</i> spp. (B)	25	33	54	38
<i>Rosa canina</i> agg.	.	40	46	31
<i>Hypericum perforatum</i>	50	47	31	23
<i>Lotus corniculatus</i>	50	13	31	54
<i>Sedum sexangulare</i>	.	47	.	62
<i>Achillea millefolium</i> agg.	75	.	38	54
<i>Lactuca serriola</i>	25	53	15	23
<i>Vicia hirsuta</i>	.	40	23	38
<i>Pilosella bauhini</i>	.	20	54	23
<i>Veronica spicata</i>	25	53	23	.
<i>Ceratodon purpureus</i> (B)	.	40	15	31
<i>Silene viscaria</i>	.	27	54	.
<i>Bryum</i> sp. (B)	25	40	23	8
<i>Dianthus carthusianorum</i>	.	20	54	8
<i>Silene nutans</i>	25	7	54	15
<i>Hieracium umbellatum</i>	75	.	46	15
<i>Securigera varia</i>	50	20	31	8
<i>Origanum vulgare</i>	50	20	38	.
<i>Petrorhagia prolifera</i>	.	20	15	31
<i>Thymus pannonicus</i> agg.	.	47	8	8
<i>Melica transsilvanica</i>	.	47	15	.
<i>Geranium sanguineum</i>	.	33	31	.
<i>Filago arvensis</i>	.	27	.	38
<i>Weissia longifolia</i> (B)	.	20	23	23
<i>Peucedanum cervaria</i>	.	20	46	.
<i>Myosotis stricta</i>	.	13	15	38
<i>Veronica arvensis</i>	.	13	8	46
<i>Poa compressa</i>	25	20	8	31
<i>Luzula campestris</i> agg.	25	7	31	23

4.1.1 Semi-dry grasslands with *Brachypodium pinnatum* (*Cirsio-Brachypodion pinnate*, *Scabioso ochroleucae-Brachypodietum pinnati*)

Diagnostic species: *Agrimonia eupatoria*, *Allium vineale*, *Arrhenatherum elatius*, *Brachypodium pinnatum*, *Ptychostomum rubens* (bryophyte, hereafter „B“), *Carex filiformis*, *Centaurea jacea*, *Dactylis glomerata*, *Euphorbia cyparissias*, *Galium verum*, *Inula salicina*, *Medicago sativa*, *Pimpinella saxifraga*, *Ranunculus polyanthemos*, *Rosa spinosissima*, *Salvia verticillata*, *Solidago virgaurea*, *Stachys officinalis*, *Trifolium montanum*, *Veronica chamaedrys* and *Viola hirta*

Constant species: *Agrimonia eupatoria*, *Achillea millefolium* agg., *Arrhenatherum elatius*, *Brachypodium pinnatum*, *Carex filiformis*, *Centaurea jacea*, *Dactylis glomerata*, *Erigeron annuus* agg., *Euphorbia cyparissias*, *Galium verum*, *Hieracium umbellatum*, *Medicago sativa*, *Pimpinella saxifraga*, *Poa pratensis* agg., *Ranunculus polyanthemos*, *Trifolium montanum*, *Veronica chamaedrys* and *Viola hirta*

Dominant species: *Brachypodium pinnatum* and *Trifolium montanum*

Semi-dry grasslands dominated by *Brachypodium pinnatum* and co-dominated by other graminoids such as *Arrhenatherum elatius*, *Carex filiformis* and *Poa pratensis* agg. It forms dense stands with a high herb-layer cover and a relatively high number of vascular plant species (on average 35 in 16 m²). The moss layer has a low cover, often formed of *Oxyrrhynchium hians* or *Ptychostomum rubens*. This vegetation occurs on sunny slopes located close to the mountainous areas of the Eastern Carpathians.

Concerning the syntaxonomical classification, we suggest this cluster to be assigned to the association *Scabioso ochroleucae-Brachypodietum pinnati* Klika 1933. This association is relatively common in central Germany, Bavaria and Austria (WILLNER et al. 2019), the Czech Republic (CHYTRÝ et al. 2007) and Slovakia (ŠKODOVÁ et al. 2014). WILLNER et al. (2019) also suggest its rare occurrence in Slovenia, northern Hungary, south-eastern Poland, Serbia, Romania and central Ukraine. Within the *Cirsio-Brachypodion pinnati* alliance, this association has a sub-oceanic distribution and is characterised by the absence of typical Pannonian and continental species. This is the second record of the association from Ukraine in addition to a record from the south of the Zakarpattia Oblast near the village of Bila Tserkva in the Tysa River valley east of our study area (ŠKODOVÁ et al. 2015).

4.1.2 Volcanic slope steppes with *Festuca pseudodalmatica* (*Festucion valesiacae*, *Festucetum pseudodalmaticae*)

Diagnostic species: *Cota tinctoria*, *Festuca pseudodalmatica*, *Galium glaucum*, *Hylotelephium maximum*, *Seseli osseum*, *Stachys recta*, *Teucrium chamaedrys*, *Trifolium arvense* and *Valerianella locusta*

Constant species: *Arenaria serpyllifolia*, *Cerastium brachypetalum*, *Cota tinctoria*, *Festuca pseudodalmatica*, *Galium glaucum*, *Hylotelephium maximum*, *Lactuca serriola*, *Potentilla argentea*, *Stachys recta*, *Trifolium arvense* and *Veronica spicata*

Dominant species: *Festuca pseudodalmatica*

Dry grasslands dominated by *Festuca pseudodalmatica*, *Galium glaucum* and *Phleum phleoides* are well developed on Chornahora Hill near Vynohradiv, on the Mukacheve Hills and near the village of Onokivtsi. This vegetation type occurs mostly on south-facing and-site slopes with shallow soil and rock outcrops. Such environmental conditions allow the development of early spring synusia of ephemeral annuals including *Arenaria serpyllifolia*, *Cerastium brachypetalum*, *Myosotis ramosissima*, *Valerianella locusta* and *Veronica verna* agg. The moss layer usually covers up to 5% of the plot area, comprising drought-adapted acidophilous species such as *Bryum* spp., *Ceratodon purpureus*, *Racomitrium canescens* and *Weissia* spp.

Table 3. Selected environmental and vegetation characteristics of the four associations *Scabioso-Brachypodietum* (S-B), *Festucetum pseudodalmaticae* (Fp), *Astero-Festucetum* (A-F) and *Airo-Vulpium* (A-V). Mean, minimal and maximal values are given. The upper indices next to the mean values indicate homogeneous groups (Tukey's test, $p < 0.05$; in case of Borhidi indicator values: multiple t -test, $p_{adjusted} < 0.05$). No indices are given where the results of the general ANOVA test or in case of BIV the modified permutation test (ZELENÝ & SCHAFFERS 2012) were non-significant.

Tabelle 3. Ausgewählte Umwelt- und Vegetationscharakteristika der vier Assoziationen *Scabioso-Brachypodietum* (S-B), *Festucetum pseudodalmaticae* (Fp), *Astero-Festucetum* (A-F) und *Airo-Vulpium* (A-V). Mittelwerte, Minima und Maxima sind angegeben. Die hochgestellten Buchstaben stehen für homogene Gruppen (Tukey-Test, $p < 0.05$; bzw. für die Borhidi-Zeigerwerte: multipler t -test, $p_{adjusted} < 0.05$). Keine Buchstaben sind angegeben, wenn die Varianzanalyse bzw. der modifizierte Permutationstest nach ZELENÝ & SCHAFFERS (2012) im Falle der Zeigerwerte keine signifikanten Muster ergaben.

Association		S-B	Fp	A-F	A-V	Association		S-B	Fp	A-F	A-V
Number of relevés		4	15	13	13	Number of relevés		4	15	13	13
Soil depth (cm)	mean	30 ^a	13 ^b	25 ^a	12 ^b	Moss layer cover (%)	mean	2	12	3	15
	min.	14	5	12	4		min.	0	1	0	0
	max.	35	35	35	35		max.	5	35	20	50
Soil pH (H ₂ O)	mean	6.3	5.5	6.0	5.5	Number of vascular plant species	mean	34.5	26.4	26.7	31.3
	min.	6.0	4.9	4.9	4.8		min.	28	20	23	17
	max.	6.6	6.7	7.4	6.4		max.	44	34	35	48
Altitude	mean	188 ^{ab}	241 ^a	196 ^{ab}	168 ^b	Number of bryophyte species	mean	1.8	4.8	3.3	4.2
	min.	157	137	128	125		min.	0	2	0	2
	max.	214	335	261	255		max.	4	9	6	10
Slope (°)	mean	19	24	14	16	BIV light	mean	7.0	7.7	7.5	7.7
	min.	10	3	2	0		min.	7.2	8.1	7.8	8.0
	max.	25	38	35	60		max.	6.5	7.3	7.0	7.4
Radiation index	mean	91	90	88	90	BIV temperature	mean	6.7	6.8	6.9	6.2
	min.	89	72	71	88		min.	6.8	7.2	7.2	6.7
	max.	97	97	96	95		max.	6.5	6.3	6.5	5.4
Heat load index	mean	89	89	88	88	BIV moisture	mean	4.3	4.6	4.6	4.1
	min.	75	65	77	67		min.	4.4	5.2	5.3	4.5
	max.	94	96	97	97		max.	4.1	4.2	4.0	3.7
Max. herb layer height (cm)	mean	68 ^{ab}	85 ^a	64 ^{ab}	44 ^b	BIV reaction	mean	4.3 ^a	2.9 ^b	3.5 ^c	3.4 ^c
	min.	60	40	40	35		min.	4.5	3.4	4.2	4.5
	max.	90	130	100	60		max.	4.2	2.5	2.8	3.0
Mean herb layer height (cm)	mean	36 ^a	33 ^a	32 ^a	15 ^b	BIV nutrients	mean	5.5	6.0	5.9	5.8
	min.	25	10	20	7		min.	5.6	6.3	6.3	6.2
	max.	40	70	50	25		max.	5.2	5.7	5.5	5.6
Herb layer cover (%)	mean	88 ^a	54 ^b	66 ^{ab}	60 ^b						
	min.	80	35	35	25						
	max.	90	80	95	90						

Syntaxonomically this cluster corresponds to the association *Festucetum pseudodalmaticae* Mikyška 1933, representing acidophilous rocky grasslands with a low abundance of sub-Mediterranean species, in contrast to the *Inulo oculi-christi-Festucetum pseudodalmaticae* Májovský et Jurko 1956, which is distributed mostly in central Slovakia and is richer in sub-Mediterranean species. The *Festucetum pseudodalmaticae* is reported from southern and eastern Slovakia and northern Hungary as a relatively common vegetation type (DÚBRAVKOVÁ et al. 2010, BORHIDI et al. 2012, ŠKODOVÁ et al. 2014), but it has not been reported from Ukraine and Romania so far (for Romania compare COLDEA & SÂRBU 2012).

The Eastern Carpathians probably represent the eastern distribution limit of this association; further sites could possibly be found on volcanic hills in the adjacent areas of north-western Romania.

4.1.3 Acidophilous dry grasslands with *Festuca stricta* subsp. *sulcata* (*Koelerio-Phleion phleoidis*, *Astero linosyris-Festucetum rupicolae*)

Diagnostic species: *Calamagrostis epigejos*, *Festuca stricta* subsp. *sulcata*, *Filipendula vulgaris*, *Galatella linosyris*, *Inula ensifolia*, *Koeleria macrantha*, *Peucedanum oreoselinum* and *Verbascum chaixii* subsp. *austriacum*

Constant species: *Calamagrostis epigejos*, *Cerastium brachypetalum*, *Dianthus carthusianorum*, *Eriogon annuus* agg., *Festuca stricta* subsp. *sulcata*, *Pilosella bauhini*, *Silene nutans*, *S. viscaria* and *Weissia* spp. (B)

Dominant species: *Festuca valesiaca*, *Inula ensifolia* and *Peucedanum cervaria*

Acidophilous grasslands dominated by *Festuca stricta* subsp. *sulcata*, *Koeleria macrantha*, thermophilous species such as *Cerastium brachypetalum*, *Galatella linosyris* and *Inula ensifolia* and acidophilous species such as *Phleum phleoides* or *Trifolium arvense* are developed on less acidic soils than those of the *Festucetum pseudodalmaticae*. The sites covered by these grasslands are, in most cases, abandoned pastures or even arable land. Currently they are locally irregularly burnt to prevent overgrowing by shrubs. We hypothesize that the lack of grazing, currently replaced by burning, supports forest-fringe specialists such as *Geranium sanguineum*, *Peucedanum cervaria* and *P. oreoselinum*; thus, some relevés from this cluster are transitional towards acidophilous variants of the forest-fringe vegetation of the *Geranium sanguinei* (e.g. relevés 30 and 31). The vegetation of this cluster is relatively common in the study area. It was observed near Berehove, Mukacheve and Uzhhorod.

We classify this vegetation to the association *Astero linosyris-Festucetum rupicolae* Maglocký in Chytrý et al. 1997. So far, the association has been reported only from the Lesser Carpathians (Malé Karpaty Mts) in south-western Slovakia (CHYTRÝ et al. 1997). MICHÁLKOVÁ (2007) pointed out that some grasslands around the Tribeč Mts in western Slovakia are very similar to this association. ŠKODOVÁ et al. (2014) merged this association with the *Potentillo heptaphyllae-Festucetum rupicolae* and called it by the latter name for priority reasons. It is obvious that the delimitation of the *Astero-Festucetum* (described from the Pannonian region in Slovakia) vs. the *Potentillo-Festucetum* (described from the Hercynian region in Bohemia) needs further study. Preliminarily we accept here the *Astero-Festucetum* as a Pannonian vicariant of the Hercynian *Potentillo-Festucetum*.

4.1.4 Nutrient-poor dry grasslands with *Vulpia myuros* (*Thero-Airion*, *Airo-Vulpietum*)

Diagnostic species: *Anthemis arvensis*, *Bromus hordeaceus*, *Carex hirta*, *Centaurea stoebe*, *Crataegus* sp., *Plantago lanceolata*, *Sanguisorba minor*, *Scleranthus annuus*, *Syntrichia ruralis* (B) and *Vulpia myuros*

Constant species: *Achillea millefolium* agg., *Arenaria serpyllifolia*, *Bromus hordeaceus*, *Centaurea stoebe*, *Crataegus* sp., *Eriogon annuus* agg., *Lotus corniculatus*, *Plantago lanceolata*, *Poa pratensis* agg., *Potentilla argentea*, *Scleranthus annuus*, *Sedum sexangulare*, *Trifolium arvense* and *Vulpia myuros*

Dominant species: *Thymus pulegioides* and *Vulpia myuros*

Some steep slopes with acidic soils are covered by nutrient-poor early-successional vegetation dominated by therophytes such as *Arenaria serpyllifolia*, *Bromus hordeaceus*, *Scleranthus annuus* and *Vulpia myuros*. This vegetation is developed on shallow gravelly soils.

It is characterised by low biomass production, with a maximum development in early to middle spring, which is followed by drought. The nutrient deficit is most likely caused by a combination of andesite bedrock, extensive grazing (mainly by goats) and soil leaching due to relatively high precipitation. We observed this vegetation type near the villages of Mala Kopanya, Onok and Veryatsya near Vynohradiv and on the Mukacheve and Berehove Hills. Other stands of this vegetation type can be found on edges of abandoned andesite quarries near the villages of Siltse and Onokivitsi and near Uzhhorod. This vegetation type is relatively common in the study area.

Besides therophytes, this vegetation contains some perennials such as *Centaurea stoebe*, *Potentilla argentea*, *Sedum sexangulare* and *Thymus pulegioides*. Therefore, we suggest its assignment to the *Airo-Vulpietum* Paucă 1941, as opposed to the *Vulpietum myuri* Philippi 1973, which is composed mainly of therophytes and confined to more humid soils (COLDEA & SÂRBU 2012). The association *Airo-Vulpietum* occurs in Slovakia (VALACHOVIČ & MAGLOCKÝ 1995), Poland (BORHIDI et al. 2012), Romania (COLDEA & SÂRBU 2012) and Hungary (BORHIDI et al. 2012). It has not been reported from Ukraine so far.

4.2 Proposed syntaxonomical scheme

Class: *Festuco-Brometea* Br.-Bl. et Tüxen ex Soó 1947

Alliance: *Cirsio-Brachypodion pinnati* Hadač et Klika ex Klika 1951

Association: *Scabioso ochroleucae-Brachypodietum pinnati* Klika 1933

Alliance: *Festucion valesiacae* Klika 1931

Association: *Festucetum pseudodalmaticae* Mikyška 1933

Alliance: *Koelerio-Phleoin phleoides* Korneck 1974

Association: *Astero linosyris-Festucetum rupicolae* Maglocký in Chytrý et al. 1997

Class: *Sedo-Scleranthetea* Br.-Bl. 1955

Alliance: *Thero-Airion* Tüxen ex Oberdorfer 1957

Association: *Airo-Vulpietum* Paucă 1941

4.3 Remarkable dry grassland sites in the Transcarpathian Lowland

4.3.1 Chornahora Hill

Chornahora is a solitary volcanic hill on the right bank of the Tysa River above the town of Vynohradiv. Its uniqueness has already been emphasised by PULCHART (1937), who wrote about unmanaged forest-steppe patches. The hill is formed of andesite and covered mostly by beech and oak-hornbeam forests on its top and north- and east-facing slopes. The vegetation cover of the south- and west-facing slopes is diverse. Lower elevations are characterised by recreational cabins with small gardens and vineyards, many of them abandoned. The forest above them is predominantly thermophilous oak forest dominated by *Quercus petraea* (alliance *Quercion petraeae*), while ravines support a *Tilia cordata*-dominated forest (alliance *Tilio platyphylli-Acerion*). Large steppe patches occur on south-facing slopes, bordering on the oak forest. As there is no evidence of former cultivation (R. Kish, pers. comm.), we conclude that the distribution pattern of oak forest and slope steppe is probably an example of a natural exposure-related forest-steppe mosaic (HAIS et al. 2016, CHYTRÝ 2019). The dry grassland vegetation of the open patches (association *Festucetum pseudodalmaticae*) is dominated by narrow-leaved grasses like *Festuca pseudodalmatica* and *Stipa pulcherrima* subsp. *crassiculmis* and other herbaceous species such as *Carduus collinus*,

Cynoglossis barrelieri, *Galium glaucum*, *Geranium sanguineum*, *Petrorhagia saxifraga*, *Phleum phleoides*, *Stachys recta* and *Thymus pannonicus* agg. Rock outcrops provide a niche for winter annuals and vernal ephemerals such as *Anisantha tectorum*, *Arenaria serpyllifolia*, *Cerastium brachypetalum* and *Valerianella locusta*. Thermophilous scrub with *Cornus mas*, *Spiraea chamaedryfolia* or *Ulmus minor* occurs along oak-forest edges.

The forest-steppe mosaic on Chornahora harbours many thermophilous species, some of them with very few or a single locality in Ukraine, e.g. *Doronicum hungaricum*, *Fraxinus ornus* and *Tilia tomentosa* (DIDUKH 2009). The Ukrainian Red Data Book (DIDUKH 2009) also mentions the local endemic species *Stipa transcarpatica*, which is supposed to be found exclusively on Chornahora Hill. However, we observed only *Stipa pulcherrima* subsp. *crassiculmis* (revised by J. Danihelka) in this area.

Unlike most other sites of dry grasslands in the Zakarpattia Oblast, steppe patches on Chornahora are not significantly affected by alien species except for the planted *Iris germanica*. The grasslands are hardly accessible due to difficult terrain and absence of roads; thus, they are rarely visited by local people or tourists. The mosaic of steppe patches and thermophilous oak forest is of high conservation value; however, the diversity of natural vegetation at this site does not seem to be endangered at present.

4.3.2 Mukacheve Hills

Volcanic hills near the town of Mukacheve are a historically well-known botanical site (MARGITTAI 1933). The hills north of the town, namely Lovachka Hill (Fig. 3e) and Halish Hill, have extensive andesite outcrops, whereas the hill south of the town (formerly named “Pál-hegy” in Hungarian literature) is covered by volcanic tuff. Large parts of Halish and Pál-hegy are occupied by recreational cabins and gardens. Lovachka Hill is free of human settlement, and treeless vegetation is sometimes deliberately burned there to prevent the development of shrubs (R. Kish, pers. comm.). The steepest slopes with grasslands (predominantly association *Festucetum pseudodalmaticae*) are dominated by *Cota tinctoria* and *Festuca pseudodalmatica*, accompanied by annual species such as *Lappula squarrosa*. The surrounding habitats are nutrient-richer, supporting specialist species of thermophilous herbaceous forest fringes such as *Dichoropetalum carvifolia*, *Geranium sanguineum* and *Laser trilobum*. We also observed a few stands dominated by *Festuca pseudodalmatica*, but co-dominants included *Bromus hordeaceus*, *Sanguisorba minor*, *Scleranthus annuus* and *Vulpia myuros*. We assigned this vegetation to the association *Airo-Vulpietum*, but there are also successional transitions to the *Festucetum pseudodalmaticae*.

The top of Pál-hegy is covered by a species-rich mosaic of thermophilous basiphilous vegetation. Light oak forests (alliance *Quercion pubescenti-petraeae*) harbours numerous basiphilous species, e.g. *Cephalanthera longifolia*, *Geranium sanguineum*, *Inula hirta*, *Laserpitium latifolium*, *Trifolium rubens* and *Verbascum phoeniceum*. Dry grasslands (*Astero-Festucetum*) are dominated by *Festuca stricta* subsp. *sulcata* and dicot herbs, e.g. *Galium glaucum*, *Peucedanum oreoselinum* and *Trifolium alpestre*.

Most of the grassland communities around the town of Mukacheve are threatened by the cessation of management and subsequent encroachment of shrubs, such as *Prunus* spp. and *Rosa canina* agg., and a succession of oak forests. Invasive alien species are also spreading, including the trees *Ailanthus altissima* and *Robinia pseudoacacia* and the herb *Erigeron annuus* agg.



Fig. 3. **a)** *Scabioso ochroleucae-Brachypodietum pinnati* near the village of Perechyn in the Upper Uzh River valley; **b)** *Festucetum pseudodalmaticae* with tussocks of *Festuca pseudodalmatica* on Chornahora Hill near Vynohradiv; **c)** *Astero linosyris-Festucetum rupicolae* dominated by *Dianthus carthusianorum*, *Festuca stricta* subsp. *sulcata* and *Inula ensifolia* near the village of Muzhievo in the Berehove area; **d)** *Airo-Vulpietum* dominated by *Potentilla argentea*, *Scleranthus annuus* and *Vulpia myuros* with patches of *Thymus pannonicus* agg. near the village of Veryatsya in the Vynohradiv area; **e)** Exposure-related forest-steppe on Lovachka Hill above the town of Mukacheve with *Festucetum pseudodalmaticae* and *Airo-Vulpietum*; **f)** A mosaic of *Festucetum pseudodalmaticae* grassland and thermophilous scrub near Onokivtsi (Photos: a) M. Chytrý, May 2017; b), d), f) K. Chytrý, May 2017; c), e) K. Chytrý, June 2016).

Abb. 3. **a)** *Scabioso ochroleucae-Brachypodietum pinnati* nahe Perechyn im oberen Uzh-Tal; **b)** *Festucetum pseudodalmaticae* mit Horsten von *Festuca pseudodalmatica* auf dem Chornahora-Hügel nahe Vynohradiv; **c)** *Astero linosyris-Festucetum rupicolae* mit Dominanz von *Dianthus carthusianorum*, *Festuca stricta* subsp. *sulcata* und *Inula ensifolia* nahe Muzhievo in der Region Berehove; **d)** *Airo-Vulpietum* mit Dominanz von *Potentilla argentea*, *Scleranthus annuus* und *Vulpia myuros* sowie Gruppen von *Thymus pannonicus* agg. nahe Veryatsya in der Region Vynohradiv; **e)** Expositionsbedingte Waldsteppe auf dem Lovachka-Hügel oberhalb von Mukacheve mit dem *Festucetum pseudodalmaticae* und dem *Airo-Vulpietum*; **f)** Mosaik aus dem *Festucetum pseudodalmaticae* grassland und thermophilen Gebüsch nahe Onokivtsi (Autoren der Fotos s. o.).

4.3.3 Berehove Hills

The hills north (Ardov Hill) and east (Kuklya Hill) of the town of Berehove lie in the warmest and driest part of the Transcarpathian Lowland. Large areas of their gentle slopes are under cultivation or used to be cultivated in the past. The bedrock consists mostly of tuff and pumice and in a few places also of a soft sedimentary Miocene limestone. There are several active or abandoned quarries and several colonies of recreational cabins. Most of the area is covered by thermophilous oak forest (*Aceri tatarici-Quercion*). A part of Kuklya Hill was terraced for wine growing but then abandoned, and currently there is an ongoing fast succession towards a scrub of *Rosa canina* agg., a tall grassland of *Calamagrostis epigejos*, and stands of invasive trees such as *Ailanthus altissima* and *Robinia pseudoacacia*. The locality harbours populations of the rare species *Rosa gallica* and *Trifolium rubrum*. The top and the northern part of Kuklya Hill in the surroundings of a quarry and the southern and eastern slopes of Ardov Hill are covered by a dry grassland of the association *Astero linosyris-Festucetum rupicolae* dominated by *Festuca stricta* subsp. *sulcata*, *Inula ensifolia*, *Koeleria macrantha* or *Phleum phleoides*. Dry grasslands on Ardov Hill are dominated by *Genista germanica* and *Silene viscaria*, while some parts of Kuklya Hill host vegetation of the *Airo-Vulpietum* dominated by *Koeleria macrantha* and *Vulpia myuros*.

4.3.4 Onokivtsi

The south-facing valley slopes, with abandoned quarries and natural rock outcrops, above the river Uzh near the village of Onokivtsi are another historically known site of the exposure-related forest-steppe in the Transcarpathian Lowland (BUČEK 1932). The site is situated relatively deep in the Carpathians foothills; therefore, it receives higher precipitation than the other study sites. Lower elevations of the valley slopes are covered by oak-hornbeam (alliance *Carpinion betuli*) and scree (alliance *Tilio-Acerion*) forests, and there is a thermophilous scrub-steppe mosaic above them. The lower fringe of the mosaic is dominated by scrub (alliances *Berberidion vulgaris* and *Prunion fruticosae*) including thermophilous species such as *Cornus mas*, *Cotoneaster melanocarpus* agg., *Prunus spinosa*, *Rosa spinosissima* and *Spiraea media*. Dry grasslands are dominated by the grasses *Elytrigia intermedia*, *Festuca stricta* subsp. *sulcata* and *Phleum phleoides* and various dicot herbs such as *Galium glaucum*, *Stachys recta*, *Teucrium chamaedrys* and *Thymus pannonicus* agg. Above is mosaic there is an oak forest (alliance *Quercion pubescenti-petraeae*). The quarry edges and sites surrounding the footpath above them are covered by *Airo-Vulpietum* vegetation. This vegetation is relatively species-rich in both vascular plants and bryophytes (on average 40 species in 16 m²).

This scrub-steppe mosaic is not managed at present, and the current development of scrub may cause serious losses of steppe habitats and their species diversity. An introduction of conservation management involving the control of shrub expansion would be highly desirable. We did not observe invasion of alien woody plants at this site, but the steppe vegetation is invaded by *Erigeron annuus* agg.

4.4 Other sites of dry grasslands

Besides the four above-mentioned most remarkable sites, we also observed dry grasslands at some other sites in the Transcarpathian Lowland. Above the andesite quarry near the village of Siltse, we found a poorly developed stand of the *Festucetum pseudodalmaticae* in an area of only ~20 m². Stands of the *Airo-Vulpietum* occurred nearby. In the surroundings

of Vynohradiv near the village of Veryatsya, we observed well-developed vegetation of the *Airo-Vulpietum*. Livestock grazing prevents succession at this site. Other stands of the *Airo-Vulpietum* are developed on shallow soils near the village of Onok and in an abandoned quarry near Uzhhorod. Several sites of the *Astero-Festucetum rupicolae* were found between Uzhhorod and Vynohradiv, in the abandoned quarry in Uzhhorod and on deforested south-facing slopes near the village of Kholmets'. The grasslands at the latter site were formerly managed, but now they are abandoned; as a result, shrubs and competitive herbs typical of herbaceous forest fringes are spreading. Near the village of Perechyn in the Uzh River valley, we observed a site with the *Scabioso-Brachypodietum*. This vegetation is developed on sandstone (flysch), which is slightly less acidic than the bedrocks at other sites.

5. Discussion

Our study provides an overview of the diversity of dry grassland vegetation in the Transcarpathian Lowland of Ukraine. The area is a part of the Pannonian Basin, although FEKETE et al. (2016) do not include it into the Pannonicum biogeographic region and refer to it as a transitional zone between the Pannonicum and the Eastern Carpathians. Before World War II the area was floristically explored by Hungarian and Czech botanists, who reported most of the dry grassland species currently known from there. However, there were no vegetation data on dry grasslands (WILLNER et al. 2017), and recent finds of the thermophilous species *Geranium lucidum* (new to the Zakarpattia Oblast; NOVÁK et al. 2017) and *Galium divaricatum* (new to Ukraine; NOVÁK & ZUKAL 2018) suggest that the diversity of the thermophilous vegetation in the Transcarpathian Lowland is still not sufficiently explored – not even floristically.

The current study covers the whole distribution range of dry grasslands in the Transcarpathian Lowland. The adjacent more humid basins and valleys of the Carpathians (e.g. the Khust Basin) are nearly devoid of dry grassland vegetation. With increasing altitude, open non-arable land is predominantly covered by mesophilous pastures of the class *Nardetea strictae* and mesic grasslands of the class *Molinio-Arrhenatheretea* (ŠKODOVÁ et al. 2015, ZAJAC et al. 2016). Consequently, the sites sampled within this study probably represent the north-eastern limit of dry grassland vegetation in the Pannonian Basin.

Dry grasslands occur especially on andesite bedrock in the study area and therefore are characterised mainly by acidophilous species. They are relatively similar to those found in nearby eastern (MÁJOVSKÝ 1955) and central Slovakia (MIKYŠKA 1933), though they are lacking several Pannonian species (e.g. *Allium flavum*, *Orlaya grandiflora* and *Pulsatilla grandis*). The Eastern Carpathians are an important migration barrier for dry grassland species. Therefore, the relevance of the described vegetation types for other parts of Ukraine is probably low. On the eastern foothills of the Ukrainian Carpathians, the predominant bedrock are flysch sediments, while volcanic bedrock is absent there. The vegetation of dry and semi-dry grasslands on flysch has a completely different structure than on volcanic hills; as a result, grasslands on the eastern foothills have a different species composition with significant presence of easterly distributed species of Pontic steppes (KUZEMKO et al. 2014, ROLEČEK et al. 2014, WILLNER et al. 2017, 2019).

In Central Europe the acidophilous dry grasslands have been traditionally classified to *Koelerio-Phleion phleioidis* (KORNECK 1974, CHYTRÝ et al. 2007, DÚBRAVKOVÁ et al. 2010). However, there are many variants of acidophilous dry grasslands of the alliance *Festucion valesiacae* (ŠKODOVÁ et al. 2014), and the boundary between them and the

alliance *Koelerio-Phleion* is still unclear. The delimitation needs further research, including field sampling of the remaining unexplored areas within the dry grassland distribution range in eastern and south-eastern Europe. An example of such a poorly explored area are the volcanic hills in north-western Romania.

Most dry grasslands in the Transcarpathian Lowland except the stands of the *Airo-Vulpietum* are currently unmanaged. The management cessation has a negative impact especially on the *Astero-Festucetum* and *Scabioso-Brachypodietum* vegetation, which is threatened by shrub encroachment. In contrast, stands of the *Festucetum pseudodalmaticae* are rather stable, even if unmanaged. However, both the *Festucetum pseudodalmaticae* and the *Airo-Vulpietum* are threatened by invasions of alien species, mainly *Erigeron annuus* agg.

Erweiterte deutsche Zusammenfassung

Einleitung – Viele Trockenrasentypen in Mitteleuropa sind abhängig von menschlicher Nutzung und daher durch Nutzungsaufgabe gefährdet. Während mitteleuropäische Trockenrasen im Allgemeinen gut untersucht sind, gibt es doch noch Regionen, aus denen kaum Daten vorliegen (vgl. WILLNER et al. 2017, 2019). Eine davon ist das Transkarpatische Tiefland im äußersten Westen der Ukraine. Mit dieser Studie möchten wir diese Wissenslücke schließen und verfolgen drei spezifische Ziele: 1) Erkundung der Verbreitung von Trockenrasen in der Region; 2) Klassifikation dieser Bestände in Assoziationen und 3) Charakterisierung der besonders bedeutsamen Vorkommen und ihrer Gefährdung.

Untersuchungsgebiet – Das Transkarpatische Tiefland liegt zwischen der Großen Ungarischen Tiefebene und den Ostkarpaten. Wenngleich FEKETE et al. (2016) dieses Gebiet nicht zur Pannonischen Provinz rechnen, zeigt es doch ausgeprägte floristische Beziehungen zu dieser. Biogeografisch ist das Transkarpatische Tiefland deutlich verschieden vom Rest der Ukraine (DIDUKH & SHEL'YAG-SOSONKO 2003) und zugleich Ungarn und der Ostslowakei viel ähnlicher. Trockenrasen kommen hier vornehmlich auf sauren Vulkaniten (Andesit) vor (PÉCSKAY et al. 2000). Die Jahresmitteltemperatur beträgt etwa 9,4 °C und der mittlere Jahresniederschlag etwa 850 mm (FICK & HIJMAN 2017).

Methoden – Wir fertigten 45 Vegetationsaufnahmen in Trockenrasen in der Umgebung der Orte Berehove, Mukacheve, Uzhhorod und Vynohradiv an, womit wir die wesentlichen Trockenrasengebiete der Region abdeckten. Diese Aufnahmen wurden einer Clusteranalyse mit *complete linkage* und Bray-Curtis-Distanz unterzogen und die resultierende Klassifikation in ein NMDS-Ordinationsdiagramm projiziert.

Ergebnisse – In der resultierenden Klassifikation unterscheiden wir drei Assoziationen der Klasse *Festuco-Brometea*, das *Scabioso ochroleucae-Brachypodietum pinnati* Klika 1933 (*Cirsio-Brachypodium pinnati*), das *Festucetum pseudodalmaticae* Mikyška 1933 (*Festucion valesiacae*) und das *Astero linosyris-Festucetum rupicolae* Maglocký in Chytrý et al. 1997 (*Koelerio-Phleion phleoidis*), sowie eine aus der Klasse *Sedo-Scleranthetea*, das *Airo-Vulpietum* Paucă 1941 (*Thero-Airion*). Abgesehen vom *Scabioso-Brachypodietum* stellen alle diese Assoziationen Erstnachweise für die Ukraine dar, was nicht verwundert, da sie einen pannonischen Verbreitungsschwerpunkt haben. Weiterhin identifizierten wir die folgenden vier Trockenrasengebiete als die regional bedeutendsten: (a) Steppen-„Inseln“ auf dem Chornahora-Hügel nahe Vynohradiv mit Vorkommen des *Festucetum pseudodalmaticae*. Dieses Gebiet hat einen hohen Naturschutzwert, wobei die aktuelle Gefährdung allerdings gering ist. (b) Hügel von Mukacheve mit Vorkommen des *Astero linosyris-Festucetum rupicolae* und des *Festucetum pseudodalmaticae*. (c) Hügel bei Berehove, welche früher als Weinberge genutzt wurden und jetzt überwiegend vom *Astero-Festucetum* besiedelt sind. Aktuell sind sie durch eine erhebliche und schnelle Verbuschung bedroht, vor allem durch nicht-einheimische Arten wie *Ailanthus altissima* und *Robinia pseudoacacia*. (d) Steppen-Gebüsch-Mosaik nahe Onokivtsi mit Vorkommen des *Festucetum pseudodalmaticae* und Inseln des therophytenreichen *Airo-Vulpietum*.

Diskussion – Unsere Arbeit ist die erste, welche sich detailliert mit der Trockenrasenvegetation des Transkarpatischen Tieflandes der Ukraine beschäftigt. Die festgestellten Assoziationen fehlen in den pontischen Steppen östlich der Karpaten (KUZEMKO et al. 2014, ROLEČEK et al. 2014, WILLNER et al. 2017, 2019); mithin liegen die einzigen Vorkommen des Landes im Untersuchungsgebiet. Zugleich stellt das Gebiet den nordöstlichen Arealrand dieser pannonischen Graslandgesellschaften dar. In dieser Arbeit akzeptierten wir das *Astero-Festucetum* als pannonische Vikariante des herzynischen *Potentillo-Festucetum*, doch bedarf die genaue Abgrenzung dieser beiden Assoziationen weiterer Studien. Die untersuchten Trockenrasenbestände sind aktuell mehrheitlich nicht mehr genutzt. Diese Nutzungsauffassung hat einen erkennbar negativen Einfluss, insbesondere im Fall des *Astero-Festucetum* und des *Scabioso-Brachypodietum*, bei denen Verbuschung einen Hauptgefährdungsfaktor darstellt. Dagegen sind die Bestände des *Festucetum pseudodalmaticae* und des *Airo-Vulpietum* im Allgemeinen weniger akut gefährdet, in Einzelfällen jedoch von der Invasion nicht-einheimischer Gehölzarten betroffen.

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Author contribution statement

K.C. designed the study, performed the data analyses and led manuscript writing. H.P. and K.C. measured soil pH and M.V. prepared the map. P.N., M.C. and V.K. contributed to the writing. All the authors participated in field sampling, discussed the results and critically revised the manuscript.

Supplements

Additional supporting information may be found in the online version of this article.

Zusätzliche unterstützende Information ist in der Online-Version dieses Artikels zu finden.

Supplement E1. Sorted table of all relevés.

Anhang E1. Geordnete Tabelle aller Vegetationsaufnahmen.

Supplement E2. Additional information on sampling location, date, site conditions and vegetation height.

Anhang E2. Zusätzliche Information zum Aufnahmeort, Aufnahmedatum, Standort und zur Vegetationshöhe.

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Supplement E1. Sorted table of all relevés. In the first section, diagnostic species ($\Phi > 0.5$) are shown for each association, sorted by their decreasing fidelity (Φ), while in the next section, the remaining species are sorted by their decreasing frequency in the whole table. Juvenile individuals of shrubs are indicated by “juv.” (shrub species without this abbreviation were recorded in the shrub layer).

Anhang E1. Geordnete Tabelle aller Vegetationsaufnahmen. Im ersten Teil sind diagnostische Arten ($\Phi > 0.5$) für jede Assoziation aufgeführt, sortiert nach abnehmender Treue (Φ), während im folgenden Abschnitt die übrigen Arten nach abnehmender Stetigkeit in der gesamten Tabelle sortiert sind. Jugendliche Individuen von Strauchern sind mit "juv." gekennzeichnet (Straucharten ohne diese Abkürzung wurden in der Strauchschicht aufgenommen).

[illegible]

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Supplement E2. Additional information on sampling location, date, site conditions and vegetation height: ad hoc defined region, nearest municipality, latitude, longitude, altitude, date, slope, aspect, radiation index, heat load index, mean soil depth and its standard deviation, soil pH (measured in water suspension), mean and maximal herb layer (E1) height. “na” indicates missing data. Associations are sorted as follows: *Scabioso-Brachypodietum* (1–4), *Festucetum pseudodalmaticae* (5–19), *Astero-Festucetum* (20–32) und *Airo-Vulprietum* (33–45).

Anhang E2. Zusätzliche Information zum Aufnahmeort, Aufnahmedatum, Standort und zur Vegetationshöhe: ad hoc-definierte Region, nächste Gemeinde, geographische Breite, geographische Länge, Höhe, Datum, Inklination, Exposition, Strahlungsindex, Wärmelastungsindex, mittlere Bodentiefe und seine Standardabweichung, Boden-pH (gemessen in wässriger Suspension), mittlere und maximale Höhe der Krautschicht (E1). “na” bezeichnet fehlende Daten. Die Assoziationen sind wie folgt sortiert: *Scabioso-Brachypodietum* (1–4), *Festucetum pseudodalmaticae* (5–19), *Astero-Festucetum* (20–32) and *Airo-Vulprietum* (33–45).

#	Region	Municipality	Latitude	Longitude	Altitude (m)	Date	Slope (°)	Aspect (°)	Radiation index	Heat load index	Soil depth (mean)	Soil depth (sd)	Soil pH	E1 height (mean)	E1 height (max)
1	Uzhhorod	Perechyn	22°28'07.2"	48°44'11.8"	214	14 May 2017	15	240	0.89	0.94	14.2	3.5	6.27	40	60
2	Uzhhorod	Perechyn	22°26'39.6"	48°43'33.3"	185	14 May 2017	25	190	0.97	0.93	33.9	3.3	6.61	40	60
3	Uzhhorod	Perechyn	22°26'35.7"	48°43'31.5"	157	14 May 2017	25	130	0.90	0.75	35.0	0	5.95	40	90
4	Uzhhorod	Perechyn	22°28'05.7"	48°44'10.3"	194	14 May 2017	10	230	0.90	0.93	35.0	0	6.46	25	60
5	Vynohradiv	Vynohradiv	23°02'49.1"	48°09'05.3"	199	9 June 2016	11	200	0.93	0.93	17.6	7.0	5.36	30	80
6	Vynohradiv	Vynohradiv	23°02'52.0"	48°09'06.0"	213	9 June 2016	20	260	0.83	0.93	7.7	8.2	5.38	45	130
7	Vynohradiv	Siltse	22°59'11.1"	48°17'41.0"	231	10 June 2016	23	90	0.78	0.65	4.8	3.0	5.65	15	40
8	Vynohradiv	Vynohradiv	23°03'51.4"	48°08'25.6"	335	7 June 2016	18	180	0.96	0.91	18.7	5.8	5.13	35	90
9	Vynohradiv	Vynohradiv	23°03'45.2"	48°08'23.9"	286	7 June 2016	35	190	0.97	0.92	12.7	9.9	5.67	40	90
10	Mukacheve	Mukacheve	22°41'32.9"	48°27'25.0"	213	11 June 2016	14	250	0.87	0.93	11.4	3.4	6.68	30	80
11	Mukacheve	Mukacheve	22°41'54.4"	48°27'27.4"	224	11 June 2016	28	190	0.97	0.93	10.6	4.7	5.65	70	130
12	Mukacheve	Mukacheve	22°41'39.8"	48°27'34.0"	217	11 June 2016	23	290	0.72	0.86	12.7	2.9	5.85	40	120
13	Vynohradiv	Vynohradiv	23°05'03.5"	48°08'49.9"	258	6 June 2016	3	90	0.87	0.85	7.3	3.9	5.84	40	95
14	Vynohradiv	Vynohradiv	23°03'45.2"	48°08'23.6"	286	7 June 2016	36	190	0.97	0.92	9.1	6.3	5.28	15	50
15	Uzhhorod	Onokivtsi	22°20'45.0"	48°39'30.7"	137	15 May 2017	20	190	0.96	0.93	9.0	8.1	4.97	10	40
16	Uzhhorod	Onokivtsi	22°20'12.7"	48°39'16.9"	194	15 May 2017	20	120	0.88	0.75	6.9	5.1	4.92	10	40
17	Vynohradiv	Vynohradiv	23°03'42.8"	48°08'26.0"	315	7 June 2016	38	240	0.82	0.96	18.7	8.2	5.19	40	100
18	Vynohradiv	Vynohradiv	23°05'31.8"	48°09'21.9"	186	6 June 2016	35	170	0.97	0.86	35.0	5.0	na	35	90
19	Vynohradiv	Vynohradiv	23°04'02.5"	48°08'19.9"	321	7 June 2016	30	190	0.97	0.93	11.8	4.6	5.40	40	100
20	Berehove	Muzhievo	22°43'47.4"	48°10'16.3"	128	6 June 2016	20	180	0.96	0.91	31.8	9.7	na	45	85
21	Uzhhorod	Uzhhorod	22°19'46.3"	48°36'40.8"	157	15 May 2017	15	310	0.74	0.83	35.0	0	6.06	20	60
22	Berehove	Muzhievo	22°42'31.5"	48°11'14.8"	202	6 June 2016	16	245	0.87	0.94	23.6	6.6	5.49	45	75
23	Berehove	Muzhievo	22°42'40.2"	48°11'03.7"	176	6 June 2016	35	230	0.88	0.97	13.0	na	7.32	50	100
24	Mukacheve	Mukacheve	22°45'08.3"	48°25'03.2"	220	14 May 2017	5	180	0.91	0.89	21.9	11.4	6.66	40	100
25	Berehove	Berehove	22°39'37.1"	48°13'34.9"	189	11 May 2017	15	140	0.92	0.83	11.6	3.9	4.85	25	50
26	Berehove	Berehove	22°39'44.3"	48°13'40.4"	146	11 May 2017	8	360	0.79	0.81	32.8	4.4	5.88	30	50
27	Berehove	Berehove	22°39'14.5"	48°13'46.9"	208	11 May 2017	10	200	0.92	0.92	32.7	4.7	6.82	20	55
28	Berehove	Berehove	22°39'12.3"	48°13'47.8"	204	11 May 2017	10	200	0.92	0.92	19.4	10.3	7.41	20	40
29	Uzhhorod	Kholmets	22°23'48.9"	48°31'42.1"	178	14 May 2017	10	180	0.93	0.91	29.0	8.0	5.34	40	55
30	Mukacheve	Mukacheve	22°45'01.5"	48°25'13.1"	247	14 May 2017	15	340	0.71	0.77	28.7	8.3	5.03	20	50
31	Mukacheve	Mukacheve	22°45'02.8"	48°25'10.6"	261	14 May 2017	2	90	0.87	0.86	12.3	8.2	5.46	20	50
32	Mukacheve	Mukacheve	22°45'10.9"	48°25'06.6"	235	14 May 2017	20	180	0.96	0.91	30.7	6.5	6.17	40	60
33	Vynohradiv	Mala Kopanya	23°06'39.0"	48°09'55.0"	154	13 May 2017	2	140	0.89	0.88	4.0	2.1	5.25	15	45
34	Vynohradiv	Veryatsya	23°09'41.0"	48°09'49.1"	153	12 May 2017	10	200	0.92	0.92	10.7	3.3	5.24	12	40
35	Vynohradiv	Siltse	22°59'14.3"	48°17'38.3"	222	10 June 2016	15	180	0.95	0.91	14.7	4.6	5.33	25	40
36	Vynohradiv	Siltse	22°59'13.7"	48°17'37.6"	222	9 June 2016	60	180	0.90	0.78	5.1	4.5	5.58	15	45
37	Berehove	Muzhievo	22°43'43.6"	48°10'14.9"	125	8 June 2016	0	-	0.88	0.88	na	na	na	na	na
38	Vynohradiv	Mala Kopanya	23°06'37.7"	48°09'53.4"	154	13 May 2017	35	130	0.88	0.67	12.3	5.8	6.27	15	50
39	Uzhhorod	Uzhhorod	22°19'43.5"	48°36'39.5"	153	15 May 2017	8	130	0.90	0.85	7.4	5.3	5.65	15	40
40	Vynohradiv	Mala Kopanya	23°06'31.5"	48°09'51.1"	142	8 June 2016	0	-	0.88	0.88	6.0	na	na	na	na
41	Vynohradiv	Mala Kopanya	23°06'30.1"	48°09'51.2"	142	8 June 2016	0	-	0.88	0.88	5.0	na	na	na	na
42	Uzhhorod	Onokivtsi	22°20'43.1"	48°39'30.3"	136	14 May 2017	10	210	0.92	0.93	17.3	11.3	5.60	15	60
43	Mukacheve	Mukacheve	22°41'57.0"	48°27'30.6"	255	10 June 2016	32	220	0.92	0.97	11.7	2.4	6.41	na	na
44	Vynohradiv	Veryatsya	23°09'40.6"	48°09'49.9"	181	12 May 2017	25	210	0.94	0.96	16.0	9.4	5.27	15	40
45	Vynohradiv	Onok	22°59'25.9"	48°12'32.5"	142	12 May 2017	15	240	0.89	0.94	35.0	0	4.81	7	35